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Soil biota in a megadiverse country: Current knowledge and future research directions in South Africa

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ABSTRACT

Soils are integral to agricultural productivity, biodiversity, and the maintenance of ecosystem services. However, soil ecosystem research depends on foundational biological knowledge that is often missing. In this review, we present a comprehensive, cross-taxa overview of the soil biota of South Africa. We discuss the literature and sampling methods used to assess soil biota, the available taxonomic expertise and main collections within South Africa, the availability of identification guides and online resources, and the status and distribution of described species. We include species lists for all South African soil biota and, for groups with sufficient distribution records, species richness maps. Despite South Africa being only 0.8% of the earth's terrestrial area, it contains nearly 1.8% of the world's described soil species (mean per taxon 3.64%, range 0.17–15%; $n = 36$ groups), with nematodes and earthworms showing a remarkable

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Belowground biodiversity
Taxonomy
Endemism

(6.4 and 7.7%) proportion of globally described diversity. Endemism is high for most groups, ranging from 33–92%. However, major knowledge gaps exist for most soil biota groups. While sampling has been relatively comprehensive in some areas for a few groups (particularly those with direct socioeconomic impacts), the Nama-Karoo, Northern Cape and Eastern Cape are poorly sampled. Natural soils in biodiversity hotspots, such as the Fynbos Biome, are also understudied. We argue that a more integrative approach to acquiring foundational knowledge in soil biodiversity is needed if applied soil research is to be effective in ensuring sustainable soil health. Considerable investment will be required to bring our understanding of the soil biodiversity in this megadiverse region to a level where the Millennium Development Goals can be reached.

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1. Introduction

Soils are integral to the delivery of almost every terrestrial ecosystem service on earth. Vital ecosystem functions and services such as litter decomposition, nutrient cycling and various aboveground vegetation processes are supported by soil biodiversity (Wardle et al., 2004; Gardi et al., 2009; Wall et al., 2012; Bardgett and van der Putten, 2014). Soil community composition plays a significant role in processes such as carbon cycling (Nielsen et al., 2011), while also driving soil processes and functions (Wurst et al., 2012). Soils are created and maintained by geological processes and the organisms that live in the soil, but the dynamics of these interactions are not fully understood. Making natural resource management decisions that directly affect human livelihoods requires a sophisticated understanding of ecosystem functioning. This in turn often requires knowledge of which species are involved in ecosystem functioning, where they occur, how they interact, and the resulting consequences for ecosystem services. However, our foundational knowledge of soil biodiversity is far from complete (Bini et al., 2006; Wurst et al., 2012). Worldwide, the majority of soil diversity is still unknown (Ibáñez et al., 2012), but it is clear that soil-dwelling groups form a large and important proportion of total biodiversity (Decaëns et al., 2006).

A sound foundational knowledge of soil communities is vital for agriculture, food security, bioremediation, and other sustainable land use practices (Brussaard 1998; Decaëns et al., 2006; Rüdisser et al., 2015). However, natural resource management decisions are being made without basic information on soil biota. Poor decisions can lead to reduced functionality, a reduction in ecosystem services, and, in some cases, permanent damage to ecosystems (MEA, 2005; Cardinale et al., 2012), jeopardising efforts to reach the Sustainable Development Goals for human prosperity (Griggs et al., 2013). In South Africa, apart from some work including termites, dung beetles and antlions (van Jaarsveld et al., 1998), soil dwelling groups have not been used in major decision-making for conservation or land-use planning, in large part due to the lack of monitoring resources available on which to base indicators of biodiversity (McGeoch et al., 2011).

Responses of soil biota to environmental change such as changes in land use, nitrogen deposition, climate change and invasions by alien species may lead to geographical range shifts of species and communities, and can possibly give rise to novel ecosystems (e.g. Sala et al., 2000; Blankinship et al., 2011; van der Putten, 2012). These pressures will vary globally, but areas of high biodiversity are often most at risk (Chapin et al., 2000; Bini et al., 2006). In sub-Saharan Africa, an estimated 180 million people are affected by land degradation, with an economic impact of ~$68 billion annually (Mirzabaev et al., 2014; Orgiazzi et al., 2015). Such issues are being increasingly recognised, and a key future focus of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES, http://www.ipbes.net/) will be to incorporate soil health into regional assessments of the state of biodiversity. In South Africa, one third of the land surface area and approximately

40% of all cropland is to some extent degraded (Vlek et al., 2010) affecting millions of people. South Africa is losing an estimated 300–400 million tonnes of soil annually (Huntley et al., 1989), with soil degradation identified as a major threat to agricultural sustainability (du Preez et al., 2011). Therefore, the threats to and opportunities for the future sustainable use of soils need to be understood. But the necessity of providing food security to a growing human population in the face of climate change, land transformation, biological invasions and pollution (MEA, 2005) is placing increasing pressure on South African soils. Research is urgently needed to understand how abiotic, biotic, and socio-economic factors interact to affect soil health in southern Africa, with the lack of integrated knowledge on soil biodiversity in the region posing a major current limitation to such understanding (Louw et al., 2014).

South Africa is likely a biodiversity hotspot for many soil groups. It is an area of mega-biodiversity, with extraordinarily well-documented species richness for plants (e.g. Coates-Palgrave, 2002), birds (e.g. Hockey et al., 2005), mammals (e.g. Skinner and Chimimba, 2006), reptiles (e.g. Bates et al., 2014) and amphibians (e.g. Measey, 2011). In contrast, the diversity of invertebrates in South Africa has been less well studied, and the total number of insect species is estimated to be two to three times the current number of described species (Scholtz and Chown, 1995). Despite the efforts of notable pioneering experts (e.g. Lawrence, 1953a), our knowledge is largely restricted to taxonomically well-known groups such as ants (Arnold, 1915; Robertson, 2000; Parr et al., 2003), spiders (Dippenaar-Schoeman and González Reyes, 2006; Dippenaar-Schoeman et al., 2015) and dung beetles (Scholtz et al., 2008). Well-developed keys and resources exist for some groups, e.g. arachnids, gastropods, and dung beetles (Dippenaar-Schoeman, 2014; Herbert and Kilburn, 2004; Scholtz et al., 2008), and there is current research focussing on certain mite groups (Ermilov and Hugo-Coetzee, 2012), earthworms (Plisko, 2010; Nxele et al., 2015; Plisko and Nxele, 2015), nematodes (Borgonie et al., 2011), soil-borne fungal pathogens (Crous et al., 2000), microbial communities (Visagie et al., 2014, 2015a,b; Slabbert et al., 2014; Postma et al., 2016) and mycorrhizal fungi (Turnau and Mesjasz-Przybylowicz, 2003). However, in general, whenever soil is sampled, new species are discovered (see Janion et al., 2011; Mager and Hui, 2012).

How many soil species does South Africa have, and can we describe them all? Similar questions have been posed recently for the world's biodiversity, and although estimates of global species count vary substantially (from 2 to 50 million species, see Scheffers et al., 2012; Costello et al., 2013; Sluys, 2013; Stork et al., 2015), there is some hope that recent and on-going advances in technology, particularly in the field of molecular biology (Yang et al., 2014; Orgiazzi et al., 2015) and metabolic profile analysis (Ferris and Tuomisto, 2015), may allow us to document soil biodiversity given a concerted effort (Costello et al., 2013). The soil ecosystem presents particular challenges to sampling, but advances in modern molecular techniques have led to a recent increase in soil biota studies (Decaëns et al., 2013; Porco et al., 2013). Globally, the number of taxonomic outputs is on the increase, with Asia and Latin America almost entirely responsible for this rise (Costello et al., 2013). With around a quarter of the world's biodiversity hotspots, more Africa-based taxonomists are needed. In South Africa, the need to integrate existing information and work collectively led to the formation of the Soil Ecosystem Research Group (SERG) with the aim to provide a platform for linking and promoting research on soil organisms (Louw et al., 2014). One of the first priorities identified was the need to collate and mobilise data and collections such that the state of knowledge of each group can be consolidated and compared.

This review aims to address the targets of the United Nations 2015 International Year of Soils (IYS: http://www.fao.org/soils-2015/en/) by raising awareness and increasing our understanding of the environmental roles of soil biota. Specifically, we aim to review the current state of knowledge on different soil biota groups in South Africa and to establish a consolidated reference platform for future soil health research endeavours in South Africa.

2. Materials and methods

Leading specialists and taxonomists were invited to review groups of soil-dwelling taxa in South Africa, in particular to provide information on the number of species known (including the number of endemics and known invasive species), sampling techniques used, the major collections in the region, and any conspicuous research gaps. Few of the groups are solely euedaphic (soil-dwelling), and many taxa are epidaphic (living and feeding in the loose surface earth and leaf-litter), rather than within the soil itself (endogaeic). We have restricted our focus predominantly to taxa that have important active roles to play in soil, although inevitably some of the groups also contribute to other systems. Groups have been arranged systematically (Fig. 1). Museum names used follow Hamer (2012).

For groups where sufficient species distribution records were available species richness maps were created. Occurrence data were also combined to construct a map showing the species richness of all soil fauna in South Africa. Maps were drawn in R Statistical Software (R Development Core Team, 2015) using the *raster* (Hijmans and van Etten, 2015) and *wesanderson* (Ram and Wickham, 2015) packages.

Using estimates of the global diversity of each taxon, which was either supplied by the contributing authors or from Scheffers et al. (2012), the percentage of South African fauna compared to the global fauna was estimated (Table 1). A full list of species per taxon is presented in Appendix A. These lists were used to determine the rate of species description for all soil biota in South Africa (Fig. 2).

3. Soil biota review

3.1. Bacteria and Archaea

The Bacteria and Archaea are the most abundant organisms and occupy every possible niche on Earth. The evolutionary links between the Bacteria, Eukarya and Archaea has been studied in detail, and is it widely accepted that eukaryotes are more closely related to Archaea than Bacteria (Gribaldo et al., 2010). Although thought to be too numerous to explicitly measure, estimates of the diversity of Bacteria have been made. Schloss and Handelsman (2006) estimated that the richness of soils from Alaska and Minnesota was between 2000 and 5000 operational taxonomic units per 0.5 g, of which about 20% of species are believed to be endemic. Another large-scale study revealed that the richness of bacterial diversity can be largely explained by soil pH, being highest in neutral soils and lowest in acidic soils, though this relationship varied between ecosystems (Fierer and Jackson, 2006).

Microbes play a crucial role in various ecosystem processes such as oxygenic photosynthesis, nutrient cycling, primary production and nitrogen fixation (Campbell, 2003). Soil microbes are vital components of soil nutrient cycles and are, therefore, important drivers of plant diversity and productivity in terrestrial systems (van der Heijden et al., 2008). Based on examples from elsewhere (Cho and Tiedje, 2000), and due to its rich plant diversity (Mucina and Rutherford, 2006), South Africa is likely to have a high percentage of microbial endemism (Cowan et al., 2013). These endemic microbes are likely threatened by factors such as climate change, invasive species (Sprent and Parsons,

Fig. 1. Soil groups discussed in this review. (a) Fungi (*Aspergillus clavatus*)—M. Truter, (b) Nematoda—M. Marais, (c) Protozoa—Flickr user: Picturepest*, (d) Enchytraeidae—WikiCommons user: Cherus*, (e) Tardigrada—R. Goldstein & V. Madden*, (f) Acari (*Tectocepheus velatus*)—L. Coetzee, (g) Microcoryphia—B. Marlin*, (h) Diplura—A. Murray*, (i) Protura—A. Murray*, (j) Collembola (*Isotomurus maculatus*)—C. Janion-Scheepers, (k) Oligochaeta—S. Shepherd*, (l) Amphipoda (*Talitroides topitotumbest*) C. Griffiths, (m) Gastropoda (*Achatina imaculata*)—D. Herbert, (n) Gastropoda (*Chlamydephorus sexangulus*)—D. Herbert (o) Isopoda (*Porcellio scaber*)—C. Griffiths, (p) Diplopoda (*Centrobolus* sp.)—M. Hamer, (q) Idiopidae (*Galeosoma planiscutatum*)—P. Webb, (r) Opiliones—L. Lotz, (s) Scorpiones (*Opisthacanthus* sp.) eating Chilopoda—J. Measey, (t) Pseudocorpiones—L. Deharveng, (u) Scarabaeinae (*Scarabaeus cupreus*)—Scarab Research Group, University of Pretoria, (v) Termitoidae (*Hodotermes mossambicus*)—J. Mitchell, (w) Formicidae (*Camponotus* sp.)—B. Braschler, (x_1) Hepialidae (*Eudalaca ammon*)—R. Schutte, (x_2) Gryllotalpidae (*Gryllotalpa africana*)—M. Picker/C. Griffiths, (x_3/x_4) Apidae (*Anthophora braunsiana*, and their nests)—A. Weaving, (y_1) Scincidae (*Scolotes gronovii*)—J. Measey, (y_2) Cape mole rat (*Georychus capensis*)—J. Measey. Photographs contributed by authors unless otherwise indicated (* licenced under creative commons licence).

Table 1
Summary of the number of species described for all soil taxonomic groups in South Africa and globally. The number in brackets indicates the estimated number of species expected for South Africa. Abbreviations used: ABG: Albany Museum, Grahamstown, South Africa, AMNH: American Museum of Natural History, New York, U.S.A.; ARC-PPRI: Agricultural Research Council, Plant Protection Research Institute, Biosystematics Division, Pretoria, South Africa; BMNH: British Museum of Natural History, London, U.K.; CAS: California Academy of Sciences, San Francisco, U.S.A.; ELM: East-London Museum, South Africa; FABI: Forestry and Agricultural Biotechnology Institute; MCZ: Museum of Comparative Zoology, Harvard, U.S.A; MM: McGregor Museum, Kimberley, South Africa; MNB: Museum für Naturkunde, Berlin, Germany; MHNG: Musee d'Histoire Naturelle Genève; MNHN: Museum National d'Histoire Naturelle, Paris, France; NCA: National Collection of Arachnida (ARC-PPRI); NCF: National Collection of Fungi (ARC-PPRI); NCI: National Collection of Insects (ARC-PPRI); NCN: National Collection of Nematodes (ARC-PPRI); NHMB: Naturhistorisches Museum Basel; NMB: National Museum, Bloemfontein, South Africa; NMSA: KwaZulu-Natal Museum, Pietermaritzburg, South Africa; NSNG: Natural History Museum Genoa; NWU: North-West University, Potchefstroom Campus, South Africa; RMCA: Royal Museum for Central Africa, Tervuren, Belgium; SAMC: Iziko South African Museum, Cape Town, South Africa; SMLA: W.A.K. Seale Museum, Department of Biology and Health Sciences, McNeese State University, Lake Charles, Louisiana, USA; SU: Stellenbosch University; DNMNH: Ditsong National Museum of Natural History (previously Transvaal Museum); UP: University of Pretoria, Pretoria, South Africa, ZMH: Zoologisches Museum, Hamburg University, Germany.

Taxa	Number of species described in South Africa	Percentage endemic to South Africa	Number of species described globally	Percentage of globally described species found in South Africa	Research priorities	Major collections
Fungi	651	Unknown	98,998[a]	0.65%	Natural soils, especially Fynbos, DNA barcoding, Ecology and function	NCF (ARC-PPRI), FABI, SU
Protozoa	Unknown	Unknown	1600	Unknown	Basic taxonomy and distribution	None
Nematodes	441 plant + 13 EPNs	44% + 73%	7003[a]	6.40%	Sampling of natural ecosystems, especially Succulent and Nama Karoo, Fynbos, Grassland and Wetlands	NCN (ARC-PPRI)
Enchytraeidae	2	50%	676	0.29%	Taxonomy and distribution, DNA barcoding	NMSA
Earthworms	323	84%	3 700	7.73%	More sampling, effect of introduced species, DNA barcoding	NMSA
Tardigrada	37	89%	1000	3.70%	Taxonomy and distribution, DNA barcoding	NMSA, SMLA
Gastropoda	525 (<600)	80%	24,500	2.14%	Functional roles, undersampled areas	NMSA, ELM, SAMC
Isopoda	127	~95%	3600	3.52%	Taxonomy and distribution, ecology, distribution of introduced species	ARC-PPRI
Amphipoda	7	70%	120	5.6%	Life history and ecology, distribution of introduced species	SAMC, NM, DNMNH
Diplopoda	154 (900–1300)	80%	12,000 (80,000)	1.28%	DNA barcoding, functional roles	NMSA, SAMC, NMB, DNMNH
Chilopoda	111 (180–200)	Unknown	3000 (5000–6000)	3.70%	DNA barcoding, functional roles	None
Pauropoda	4	Unknown	<500	0.80%	Taxonomy and distribution, functional roles	None
Symphyla	4	Unknown	<500	0.80%	Taxonomy and distribution, functional roles	None
Araneae	2170 (1331 associated with soil)	60%	45,846[b]	4.73%	Distribution data, especially for North West, Northern Cape and Eastern Cape Provinces	AM, BMNH, CAS, MNHN, NCA (ARC-PPRI), NMB, NMSA, RMCA, SAMC, DNMNH
Opiliones	208	92%	6400	3.25%	Need for taxonomists and revisions of the major genera, sampling gaps, collect from type localities	MCZ, NCA, NMB, NMSA, SAMC, DNMNH
Scorpiones	101	57%	~2000	5%	Systematic revisions using an integrative approach, additional surveys, studies on ecology, life history and behaviour	AMNH, BMNH, CAS, MM, MNB, MNHN, NCA, NMB, NMSA, RMCA, SAMC, DNMNH, ZMH
Pseudoscorpiones	135	70%	3500	3.85%	Biology and diversity	NCA, NMB
Oribatida	434 (1000)	~75%	10,000	4.34%	Ecology, identification keys	NMB
Mesostigmata	281	~50%	19,100	1.47%	Ecology, identification keys	ARC-PPRI, NMSA, NWU
Trombidiformes	700	~50%	22,000	3.18%		ARC-PPRI, NMSA, NWU
Microcoryphia	22	95%	520	4.04%	Taxonomy and distribution	None
Diplura	40	?	924	4.33%	Taxonomy and distribution	None
Protura	2	?	788	0.27%	Taxonomy and distribution, biology and ecology	None
Collembola	124 (1000)	60%	8200	1.42%	Taxonomy and distribution, identification keys	ARC-PPRI, SAMC
Insecta			~1,000,000[a,c]		Distributional data, knowledge on full life history requirements, conservation status, updated taxonomic information.	
Blattaria	230	Unknown	4641	4.96%		None
Termitoidae	126	33%	2929	4.3	Systematics and ecology, revision of genera including *Odontotermes*,*Microcerotermes*, *Microtermes* and *Cubitermes*, ecology, quantifying contribution to ecosystem services	ARC-PPRI
Embioptera	37	Unknown	~360	10.28		None
Orthoptera	~765	Unknown	~25,000	3.06		ARC-PPRI, DNMNH
Psocoptera	~80	Unknown	~5550	1.44		None
Hemiptera	~270	Unknown	>80,000	0.34		None
Neuroptera	~252	Unknown	~2000	12.6		ARC-PPRI
Coleoptera	~35 families ~4000	Unknown	>350,000	1.14		ARC-PPRI, SAMC, DNMNH
Scarabaeinae	491	~37%	~5800	8.47%	Attention to alpha taxonomy, more precise biogeographical and ecological data, interactions between dung beetles and other members of the soil fauna	NCI, SAMC, DNMNH, UP
Diptera	~1553	Unknown	~150,000	1.04		NMSA, SAMC
Lepidoptera	~6800	Unknown	~160,000	4.25		SAMC, DNMNH, private collections
	~20 families ~2000	Unknown	~115,000	1.74		ABG, ARC-PPRI, NMB, SAMC

Table 1 (*Continued*)

Taxa	Number of species described in South Africa	Percentage endemic to South Africa	Number of species described globally	Percentage of globally described species found in South Africa	Research priorities	Major collections
Hymenoptera (excluding Formicidae)						
Formicidae	541	33%	>13,986 (~22,000[d,e])	3.87	Revision of genera with outdated or no keys, distribution, large-scale standardized surveys of undersampled areas, general biology and interactions with other organisms	AMNH, ARC-PPRI, BMNH, CAS, MNB, NHMB, MHNG, NMB, NSNG, SAMC, DNMNH
Vertebrates	110	Unknown	61,995[a]	0.17	Impact of vertebrates on social soil invertebrate prey items, impact of expansion of urban areas on soil vertebrates and their prey items	None
Total	24,005		1,334,098	1.8		

[a] Scholtz and Holm (1986) and Scholtz and Chown (1995), while worldwide estimates are taken from Mayhew (2007).
[b] World Spider Catalogue (2016).
[c] Scheffers et al. (2012) and sources therein, see references in text.
[d] Agosti and Johnson (2003).
[e] Agosti and Johnson (2005) and Schultz (2000).

2000; Ndlovu et al., 2013) and habitat destruction. Knowledge of the microbial diversity is especially important for the conservation of these unknown communities and the terrestrial communities they support.

Microbial diversity studies in South Africa are increasing, and several institutions support research in this field. Given the advanced technologies available, such as next-generation sequencing, this trend should continue in order to discover the true diversity of microbial diversity in South African soils (Cowan et al., 2013; Slabbert et al., 2014; Postma et al., 2016).

3.2. Fungi

Fungi commonly rank as the most abundant soil micro-organisms in terms of biomass and physiological activity (Kjoller and Struwe, 1982). They are ubiquitous in the environment and fulfil a wide range of important ecological functions such as nutrient and carbon cycling and soil stabilisation (Christensen, 1989; De Boer et al., 2005). Fungi are not only decomposers, but also saprobionts, mutualists and parasites (Christensen, 1989).

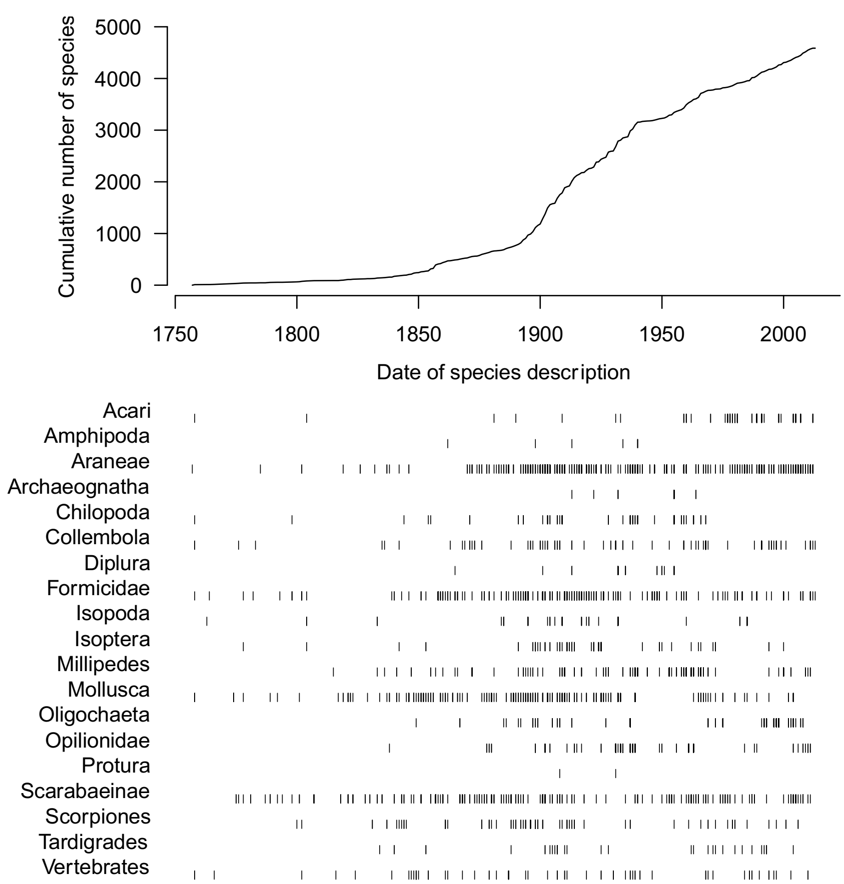

Fig. 2. Cumulative species descriptions trend for all South African soil fauna indicates the initial lag in descriptions up to the start of the 20th century. The trend in alpha taxonomy of South African soil fauna suggests that the total number of species cannot yet be estimated. Data for each of the component groups demonstrates the different trends in soil fauna taxonomy.

All major taxonomic groups of fungi are represented in soils. These include the Eurotiales, Hypocreales, Leotiales, Microascales, Mucorales, Onygenales, Pezizales, Saprolegniales, Sordiales (Bills et al., 2004) and Glomeromycota (Schüßler et al., 2001). Species diversity is influenced by microhabitat heterogeneity; intermingling of primary, secondary and tertiary decomposers; faunal grazing; persistence of organic matter that promotes niche partitioning; temporal changes in climate; and vegetation amongst other factors (Christensen 1989; Bills et al., 2004).

3.2.1. Taxonomy and collections

Fungal diversity has been documented in South Arica since 1945, when E.M. Doidge published her classic work (Doidge, 1950). This was updated by Crous et al. (2000), in which all published records for phytopathogenic fungi in South Africa were summarised. Research has also focussed on mycorrhizal fungi (Dames et al., 1999; Hawley and Dames, 2004; Hawley et al., 2008), soil-borne pathogens (Crous et al., 2000) and fungi as indicators of soil conditions (Cohen, 1949). Most of these studies focussed on economically important genera, but the vast majority of fungi are not pathogenic, and only a few studies have focussed on the fungal communities in soils (Scott, 1968; Eicker, 1969, 1970, 1973, 1976; Papendorf, 1976; Eicker et al., 1982; Lundquist and Baxter, 1985; Lundquist 1986, 1987; Visagie et al., 2009, 2013, 2014, 2015a,b; Spruyt et al., 2014).

The main collections are held at the National Collections of Fungi (NCF), Pretoria, South Africa (established in 1905), and as of 2015 this contained 61,000 herbarium specimens and 18,000 living fungal strains. Currently, 3244 soil fungal specimens from 240 genera are held in the NCF. Specimens were collected in all nine provinces but there are notable geographic biases, for example, Gauteng (63%), Limpopo (9.9%), KwaZulu–Natal (6.5%), Mpumalanga (6.8%), Western Cape (4.4%), Eastern Cape (3.4%), Northern Cape (2%); North–West (1.6%) and Free-State (1%). Essential international databases used for the identification of unknown fungal isolates and general taxonomic information are *MycoBank* (www.mycobank.org), *Index Fungorum* (www.index-fungorum.org), *Cybertruffle* (www.cybertruffle.org.uk); *UNITE* (www.unite.ut.ee) and *MaarjAM* (www.maarjam.botany.ut.ee).

Mycorrhizal fungal collections are limited to a few individual research groups. Several ericoid root-associated fungal cultures have been deposited with the NCF and the development of an African Mycorrhizal Collection is being discussed with the NCF.

3.2.2. Sampling and identification

Sampling protocols differ between environments and based on the aim of the particular study (Slabbert et al., 2010, 2013; Visagie et al., 2009, 2013; Visagie and Jacobs, 2012). In the case of ecological based community analysis of soil, a transect protocol is favoured with a number of soil samples being taken within the first 10–20 cm of the soil profile. Each of these samples can be analysed individually or the samples can be homogenised to get a representative sample for a particular site (Jeschne et al., 1990; Zeller et al., 2003). In the case of taxonomic studies, point samples are usually more than sufficient to provide adequate material for study.

Mycorrhizal research has concentrated on several mycorrhizal types, which include ectomycorrhizas (Dames et al., 1999; Hawley et al., 2008; Adeleke and Dames, 2014), arbuscular mycorrhizas (Dames, 1991; Mukasa-Mugerwa et al., 2011; Straker et al., 2010) and ericoid mycorrhizas (Straker, 1996; Bizabani, 2012). Extensive diversity studies are increasingly becoming the focus of research, while orchid mycorrhizal research has not yet been addressed. Identification has been mostly made through microscopic characterisations (Dames, 1991; Dames et al., 1999; Straker et al., 2010), and more recently these have been combined with molecular methods (Hawley et al., 2008; Bizabani, 2012; Spruyt et al., 2014).

Isolation of fungi from soil has traditionally relied on the ability to culture the different species. This has been used with great success in a number of studies and is still the method of choice when doing taxonomic research (Visagie and Jacobs, 2012; Visagie et al., 2009, 2013). With the development of molecular techniques, sequencing of key genes or barcoding markers have been used in addition to morphology for the identification and characterisation of fungal species (Visagie et al., 2009, 2013; Visagie and Jacobs, 2012). When investigating soil fungal communities, the sheer number of species and the fact that a large proportion of species are non-culturable has prompted the use of molecular methods adapted from bacteriology (Anderson and Cairney, 2004). These include the use of phospholipid fatty acids (PLFAs) to estimate the total fungal biomass in soil (Anderson and Cairney, 2004), stable isotope probing (SIP) (Lueders et al., 2004), and a number of different community fingerprinting techniques such as denaturing gradient gel electrophoresis (DGGE), temperature gradient gel electrophoresis (TGGE), single strand conformation polymorphism (SSCP), terminal restriction fragment length polymorphism (T-RFLP) and amplified ribosomal intergenic spacer analysis (ARISA) (Cannon, 1999; Anderson and Cairney, 2004; Slabbert et al., 2010). Each of these techniques has its limitations and advantages.

Recent advances in sequence technologies have facilitated analysis of environmental fungal DNA through the use of specific gene markers such as the ITS (Jumpponen et al., 2010) and 18S (Rousk et al., 2010) gene regions. The application of next-generation sequencing technologies has recently contributed vast amounts of data to ecological and environmental research (O'Brien et al., 2005; Damon et al., 2012). This effectively eliminates the bias towards the culturable fraction of the fungal soil and provides a total community diversity analysis. However, a major stumbling block in the application of this technique is the poor representation of many species in global sequence databases as next-generation sequencing tends to return a large number of unclassified or poorly described species (Nilsson et al., 2009; Hibbett et al., 2011).

3.2.3. Future research

Ongoing initiatives in soil fungal ecology include comprehensive studies into the effect of invasion on fungal communities, the role of fungi in agricultural processes and natural soil processes, and the distribution of species in natural soils of different biomes. Natural soils in South Africa, particularly in biodiversity hotspots such as the fynbos, succulent Karoo and grassland biomes, remain largely unstudied and undocumented. These areas contain large numbers of novel species. For example, the ericoid mycorrhizas associated with *Erica* spp. (Bizabani, 2012; Straker, 1996) and *Penicillium* spp. appear to be the dominant group in fynbos soil samples, representing half the species currently known in the genus (Visagie et al., 2009, 2013, 2014, 2015a,b).

3.3. Protozoa

Protozoans are considered a sub-kingdom of the kingdom Protista, and about 50,000 species have been described from every possible habitat (Lee et al., 2000). However, only about 1600 species are known from terrestrial habitats worldwide (Foissner, 1999). Global soil protozoa diversity is predicted to be between 1330 and 2000 species (Foissner, 1997). The most updated classification, combining ultrastructure and molecular studies, was made by Adl et al., (2005, 2012).

Protozoans consume a significant portion (usually >50%) of bacterial productivity, enhance soil respiration, increase carbon and nitrogen mineralisation, and are prey for a large number of microfauna (Lee et al., 2000). Several groups of soil protozoa are recognised. Amoebae are amongst the most abundant of soil protozoa (Foissner, 1999), with about 60 species known from soils

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globally (Page, 1976). Testae amoebae are amoeboid organisms with a shell, and have a considerable species diversity and deep vertical distribution (Foissner, 1999). There are around 260 flagellate species globally. Flagellates feed on bacteria, and are very small (<20 μm) allowing them to inhabit small soil pores (Foissner, 1999). Lastly, sporozoans are parasitic organisms.

Field studies on global protozoan diversity are lacking for most regions and habitats, and even well investigated regions, such as Europe, have been shown to have a high number of undescribed species (Foissner et al., 2003). However, there is significant progress, as the number of new species being described is increasing (World Conservation Monitoring Centre, 1992). While methodological and taxonomic problems need urgent attention in this field (Foissner, 1999), the group holds some promise as an environmental indicator (Foissner, 1999).

Foissner (1997) investigated a large number of samples from Africa, Australia and Antarctica, and found that Africa had the highest diversity with 507 species, of which 240 were undescribed. He concluded that, depending on the region, 70–80% of soil ciliates are still unknown. Most collections in Africa have been done in Namibia (Foissner et al., 2002) with no known repository in South Africa and no local expertise.

3.4. Nematoda

Nematodes are among the most abundant soil organisms and are an essential part of soil ecology, influencing various aspects such as nutrient mineralisation and decomposition (Ferris et al., 2012). Certain parasitic nematodes also influence plant and animal dynamics (Yeates et al., 2009). Nematodes are often used as indicators of soil health. Nematodes can be classified into different trophic levels, namely herbivores, bacterivores, fungivores, omnivores and predators, according to their feeding patterns.

3.4.1. Taxonomy and collections

Van der Linde was the first nematologist in South Africa, and made significant contributions to developing the field and describing South African species (Van der Linde, 1938, 1956, 1959). Important South African publications include *A guide to plant and soil nematodes in South Africa*, which described 134 genera (Heyns, 1971) and *Nematology in southern Africa* (Keetch and Heyns, 1982), which is currently being revised. Subsequent significant publications include Keetch and Buckley (1984), Kleynhans (1991) and in 1996 *Plant nematodes in South Africa* was published, summarising the knowledge on the occurrence of plant nematode species (51 genera) in South Africa (Kleynhans et al., 1996).

The South African Plant–Parasitic Nematodes Survey (SAPPNS) was founded by the Nematology Unit of the ARC-PPRI in 1987 to: (i) make a comprehensive assessment of the nematode biodiversity resources of South Africa, (ii) make an inventory of all the plant-parasitic nematodes of South Africa, (iii) study the biogeography of these plant–parasitic nematodes, (iv) establish an electronic database of these plant–parasitic nematodes at the NCN, and (v) compile distribution maps (Van Vuuren, 1992; Marais, 2006). As part of the SAPPNS programme systematic surveys were undertaken in areas where little information was available on the plant nematodes of the region, especially nematode-plant associations (Marais and Swart, 1996, 1998, 2013a; Marais et al., 2004; Van den Berg et al., 2007). In 2006 the second phase of the SAPPNS was launched consisting of digitising the 188,000 specimens deposited in the National Collection of Nematodes (Marais and Swart, 2013b). From the datasets of the 9000 records in the SAPPNS database and the NCN database, 441 plant parasitic nematode species are currently reported from South Africa and 196 of these species are considered endemic to South Africa (Fig. 3).

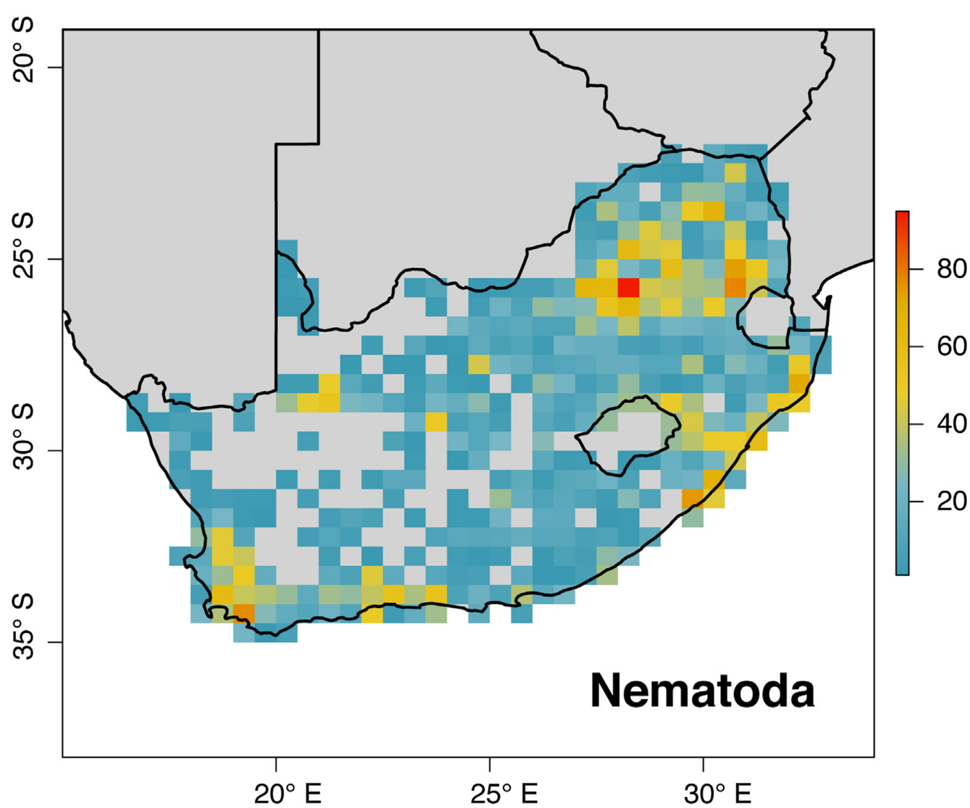

Fig. 3. Species richness distribution for nematodes in South Africa.

The Nematology Centre in Stellenbosch was established in 1963 for the study of nematodes with particular interests in the fruit and grapevine industries. More recently there has been a focus on the study of entomopathogenic nematodes (EPNs) at this centre. To date, a total of 14 EPN species have been reported of which 10 are endemic to South Africa (Nguyen et al., 2006; Malan et al., 2008; Stokwe et al., 2011; Nthenga et al., 2013; Çimen et al., 2014a,b; Malan et al., 2014, 2015; Abate et al., 2016). At the end of 2006, the Department of Zoology and Entomology at the University of the Free State established a new specialist research area in Nematology under the leadership of C. Jansen van Rensburg.

3.4.2. Sampling and identification

Samples for plant feeding and free-living nematodes are collected with a spade, a garden trowel or a soil auger depending on the type of soil in the rhizosphere of plants. Samples are placed in a plastic bag and immediately sealed, transported in cool boxes to a laboratory, and stored in a cold room at 12 °C until extraction (Kleynhans, 1997). Various techniques exist to extract plant feeding and free-living nematodes from the soil. The method that delivers the most consistent results is the sieving-centrifuging-sugar flotation technique as adapted from Kleynhans (1997) where 250 cm^3 of soil is washed though a series of sieves and centrifuged. The population size of each different trophic level (Yeates et al., 1993) and of the plant-parasitic nematodes are determined by withdrawing a sub-sample into a De Grisse counting dish, identifying the nematodes to genus level and counting the number of specimens of each genus. For rapid identification to species level, the nematodes are mounted on temporary slides and identified with a microscope by the relevant experts. To sample for EPNs in each ecosystem soil cores are taken by using an auger (2.5 × 30 cm) or a trowel (depending on if the soil is sandy or rocky) at 15 evenly distributed points or trees over an area of 1 ha. All sub samples are combined, mixed gently in the field and a 1 L sample transported in cooler bags back to the laboratory. Root samples are taken in the same way and buried in the soil sample during transport to the laboratory (no wetting) in a plastic bag. Voucher specimens of each species are prepared for fixing and mounting using the most appropriate method for the specific nematodes (De Grisse, 1969; Manẓanilla-López, 2012).

3.4.3. Invasive species

Several plant parasitic nematodes now reported from South Africa were probably brought into country with plant material, as human activity is known to be one of the principal routes for dispersal of plant parasitic nematodes. One of the most well recorded cases is that of *Meloidogyne partityla*. This root-knot nematode was described from pecan nut in Mpumalanga but was in all probability introduced with rooted seedlings from the USA as *M. partityla* are also reported southern USA (Kleynhans, 1986; Kleynhans et al., 1996).

3.4.4. Future research

Future studies should include surveying and identification of nematodes from different natural ecosystems especially Succulent and Nama Karoo, Grassland and Fynbos and with special emphasis on wetlands, as data is lacking from these areas. Surveys on the occurrence and distribution of EPNs in all provinces are needed, as comprehensive data about this group of nematodes is lacking for South Africa.

3.5. Oligochaeta

3.5.1. Enchytraeidae

Enchytraeids (sometimes known as potworms) are an important component of the soil mesofauna (together with Collembola and Oribatida) (Coleman et al., 2004). Although their size is small (typically 0.2 mm in diameter and 8 mm long), their abundance can be in the region of hundreds of thousands of individuals per square metre, and their impact on the functioning of the soil ecosystem can be expected to be equally high. The global diversity for described enchytraeids has been recently assessed as 676 species (715 taxonomic units) in 31 genera, although the actual diversity is expected to be perhaps an order of magnitude greater (Schmelz and Collado, 2010).

3.5.1.1. Taxonomy and collections. Not much is known about South African enchytraeids. Michaelsen (1913) described *Fridericia peregrinabunda* from KwaZulu–Natal, but since then there has only been one more species described from an indigenous forest near Grahamstown the Eastern Cape (*Achaeta gigantea*). This species is remarkable for its large size (up to 45.5 mm long and diameter of 1.2 mm). Both type species of enchytraeids are in the KwaZulu–Natal Museum collection (Plisko, 2006a).

3.5.1.2. Sampling and identification. The International Organisation for Standardisation (ISO) has a set methodology (ISO 23611-3) for sampling of enchytraeids (see Römbke et al., 2006b). This comprises a split core extractor (5–8 mm diameter) to a depth of around 20 cm with numerous replicates due to their aggregated distributions (Jänsch et al., 2005). In the laboratory, cores are crumbled in a sieve (mesh size 1 mm), and suspended in a bowl of cool water (10–15 °C), and the enchytraeids collected from the bowl after 1–7 days, depending on humic content (see Römbke et al. (2006a) and references therein for a detailed protocol.) Given the lack of current South African taxonomic expertise, DNA barcoding techniques are considered to be important for this group.

3.5.1.3. Future research. Given the diversity of other oligochaetes in the region (see below), South Africa is likely to also have globally important enchytraeid diversity. Research on this group should focus on basic gathering of distribution data and taxonomy. Some studies have shown important interaction effects between earthworms and enchytraeids, and this is particularly important in the light of the negative interactions reported for invasive earthworms in North America (Schlaghamerský et al., 2013).

3.5.2. Earthworms

Earthworms are probably the most familiar group of soil macrofauna, and although they probably represent only 1% of global soil animal diversity (Decaëns et al., 2006) they are known to act as ecosystem engineers through their bioperturbational activities, altering soil nutrient dynamics, augmenting plant growth, as well as playing a fundamental role in nutrient cycling (e.g. Darwin, 1882; Jouquet et al., 2006; Lavelle et al., 2006). Globally around 3700 species have been described (Hendrix et al., 2008), although global diversity probably exceeds 7000 species (Lavelle and Lapied, 2003). South Africa has 243 species in three families, of which many are endemic (Fig. 4). The Acanthodrilidae (5 genera with 107 species in Acanthodrilinae, Plisko and Nxele, 2015), Microchaetidae (4 genera, 100 species, Plisko, 2010), and Tritogeniidae (2 genera, 36 species; Plisko, 2013). Despite this remarkable annelid diversity, the country's earthworm fauna has not yet been adequately surveyed and it is likely that the number of endemic taxa may grow substantially with further research.

Earthworms have been studied in fields such as physiology (Dlamini et al., 2001; Reinecke, 1975; Viljoen and Reinecke, 1988), ecology (Ljungström and Reinecke, 1969; Reinecke and Ryke, 1970; Visser and Reinecke, 1977) and vermicomposting (Reinecke and Venter, 1987). These studies are summarized by Reinecke and Alberts (1994).

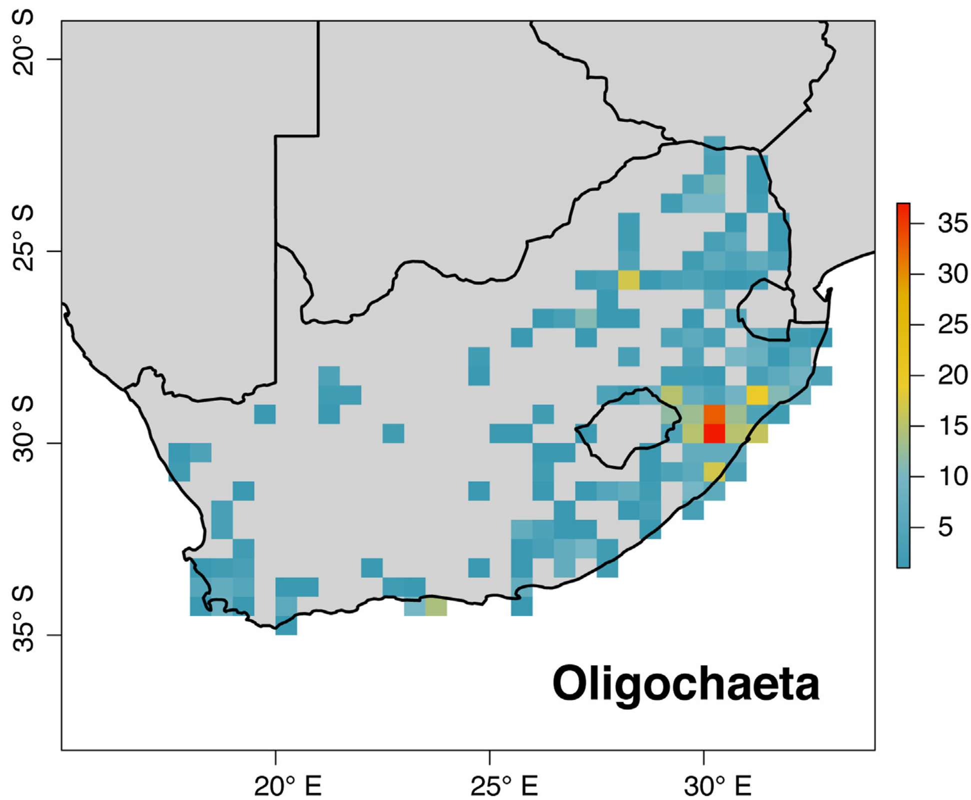

Fig. 4. Species richness distribution for earthworms in South Africa.

3.5.2.1. Taxonomy and collections. Taxonomy of South African earthworms began in 1849 with W. Rapp describing the first earthworm found in South Africa (Rapp, 1849). Between 1867 and 1899 other researchers described many new species in Acanthodrilidae and Microchaetidae (Kinberg, 1867; Beddard, 1884; Benham, 1888, 1892; Rosa, 1891, 1893, 1897, 1898; Michaelsen, 1891, 1899, 1902, 1907, 1908, 1913, 1933). Pickford's important monograph (1937) on the Acanthodrilinae, the description of new microchaetid species (1975) and the Ljungström (1972) publication on introduced earthworms brought a new light on the oligochaets in South Africa. Current knowledge has been extended by descriptions of new genera (e.g. *Michalakus* and *Kazimierzus*), and numerous new acanthodrilin and microchetid species (e.g. Plisko, 1991, 1993, 1996a, b, 2002a, b, 2003, 2012; Nxele, 2015b). The recent identification of a new family, Tritogeniidae (Plisko, 2013), and application of a molecular method (Nxele, 2015a,b) have broadly extended understanding of this taxon.

The main collection of earthworms is located at the KwaZulu–Natal Museum and includes over 6000 records. The reference collection has 139 type specimens (Plisko, 2006b; Nxele, 2015b) and includes indigenous earthworms from the families Microchaetidae, Tritogeniidae and Acanthodrilidae (Acanthodrilinae) (Plisko, 2013). The collection also includes many non-native species collected in South Africa. Plisko and Nxele are the only taxonomists currently working on South African earthworms.

3.5.2.2. Sampling and identification. A standard methodology has recently been proposed for sampling earthworms in South Africa (Nxele et al., 2015). Quantitative collections of earthworms are made by digging out 50 cm × 50 cm plots with a depth of 20 cm. Soil is then hand sorted in large plastic trays (50 cm × 50 cm). In order to try to extract deep burrowing earthworms a mustard solution with a concentration of 10 gL^{-1} is to be poured onto the dug plot. Once collected, earthworms are washed twice in clean water before being narcotised in 20% alcohol. For long term storage and morphological classification of species, specimens are fixed in 4% formalin (10% from a 40% stock solution) for at least 24 h, and then stored in 75% ethanol. Formalin fixed tissues are not suitable for DNA based analyses, and so duplicates should be collected and placed into 100% ethanol. In the case of very large specimens, small portions of tissue can be preserved (see Nxele et al., 2015 for a detailed sampling protocol). There are no current books or field guides for the identification of South African earthworms. Currently, identification of indigenous species is based mainly on the original descriptions or available limited keys (see Nxele et al., 2015; Plisko and Nxele, 2015). Recently, Nxele et al. (2015) also produced a list of key priorities for work on megadrile earthworms in South Africa. This included the compilation of an atlas and Red Data list, development of a field guide, mapping and modelling species distributions, engendering public interest through outreach, developing a DNA barcode reference library, assessing the risks of future introductions to and around South Africa, determining the status and invasive potential of introduced species, assessing the value of ecosystem services provided by earthworms under South African conditions, and the potential of species as bio-indicators of soil health.

A recent study showed that applying the methods described above mainly result in the collection of invasive taxa in South Africa, despite native taxa being present in KwaZulu–Natal, where native earthworms are very large. This necessitates additional qualitative searches for native taxa: searching as indicated by casts; searching in rotting forest wood; and opportunistic collections, especially for larger species (Nxele et al., 2015).

3.5.2.3. Invasive species. The importance of invasive earthworms on soil ecosystem dynamics has only recently received attention, with some 120 invasive species recognised globally (Hendrix et al., 2008). A recent review of invasive earthworm species in South Africa (Plisko, 2010; Plisko and Nxele, 2015) listed 44 species including representatives of six families (Acanthodrilidae (Benhamiinae), Eudrilidae, Glossoscolecidae, Lumbricidae, Megascolecidae and Ocnerodrilidae), which suggests that South Africa has representatives of all families of the world's invasive earthworms, except the Palearctic family Moniligastridae which is invasive in the Nearctic, Neotropics and Australia (Hendrix et al., 2008). For example, *Allolobophora caliginosa, Amynthas aeruginosus, A. corticis, A. gracilis, A. minimus, A. rodericensis, A. morrisi, Dendrodrilus rubidus, Octolasium lacteum* and *Pontoscolex corethrurus* are some of the species that are present in indigenous forests in Limpopo (Horn et al., 2007), protected grassland in KwaZulu–Natal (Nxele, 2012), and the savannah of the Kruger National Park (Reynolds and Reinecke, 1976; Zicsi and Reinecke, 1992). Plisko (2001) and Plisko and Nxele (2015) highlighted the potential impact of introduced species such as *Pontoscolex corethrurus* and *Dendrodrilus rubidus*, although these were not yet observed or confirmed in South African environment but have been observed elsewhere (Csuzdi and Zicsi, 2003).

3.5.2.4. Future research. A DNA Barcoding initiative has recently been established at the University of KwaZulu–Natal (Nxele, 2015a). DNA barcoding data is available from 310 specimens including six families (www.earthwormbol.org: Acanthodrilidae, Megascolecidae, Microchaetidae, Lumbricidae, Glossoscolescidae, Tritogeniidae). In addition, a revision of some species in *Tritogenia* has recently been completed (Nxele, 2015a). To date 185 specimens have been sequenced using two molecular markers (cytochrome oxidase I and 16S rRNA). Work on DNA barcoding are still at the initial stage and thus much work is still required in order to build on the existing reference library and construct a molecular phylogeny of indigenous species. There is little information on the status and invasive potential of introduced species. Surprisingly, little information is available on which species are used for vermiculture, and the dispersal pathways of these species. Risk assessments of the invasive potential and impact of exotic earthworms are desperately needed.

Overall, sampling for earthworms in South Africa is poor with only 229 (11.4%) of 2008 quarter degree grid cells (QDGCs) having records (Fig. 4). While some areas might be expected to be completely devoid of native species (e.g. deserts), there is still only a fraction of the country sampled. Of the 229 QDGCs sampled, 176 contained native species (76.9%). The best sampling cover to date was in KwaZulu–Natal, and there the coastal and scarp forests appear to represent hotspots for earthworm diversity. However, the Tsitsikamma forests also contain many taxa, and there are many more South African forests that remain unsampled. Given our global knowledge of earthworm distributions, one might speculate that the South African forests contain the highest diversity of species compared to other biomes, but more sampling is required to confirm this. Finally, there is a need to assess earthworm distribution and diversity (especially of the endemic megadriles), train more people in identification (e.g. by initiating an annual training course), and assess the potential environmental risk of vermiculture.

3.6. Tardigrada

Tardigrades, also known as waterbears, are small (average of 0.2–0.5 mm) invertebrates. They are recognised by their cylindrical, segmented bodies with four pairs of poorly articulated clawed limbs (giving rise to their characteristic bear-like crawling motion). Tardigrades occur in all freshwater, terrestrial and marine environments, from topical forests to Antarctica (McInnes, 1994). They feed on a variety of fluids through their piercing mouthparts, and can also be carnivorous, feeding on rotifers, nematodes and other tardigrades (Kinchin, 1994).

Tardigrades are famously known to have the ability to enter a resistant state to survive extreme conditions during cryptobiosis (Copley, 1998, 1999). Most studies have been on the form of cryptobiosis started by dehydration, called anhydrobiosis. This is especially prevalent in habitats such as mosses or lichens, where tardigrades will experience long periods without water, but is also often found in the soil (McInnes, 1994). The animal loses all its body water and can stay in a state like this, called a *tun*, for an extensive period of time (they have been reported to survive for over 100 years; Kinchin, 1994). In different states of cryptobiosis tardigrades have been found to survive temperatures ranging from −272.8 °C to 125 °C (Kinchin, 1994; McInnes and Norman, 1996). Some of these amazing evolutionary adaptations are being investigated for applied uses in medical fields such as cryosurgery.

3.6.1. Taxonomy and collections

More than 1000 species of tardigrades are known worldwide (Guidetti and Bertolani, 2005; Degma and Guidetti, 2007; Degma et al., 2015). Research on tardigrades in South Africa has been very sporadic, with the first records dating back to 1907 (Murray, 1907). Thereafter important contributions were made by Dastych (1980, 1992, 1993). Sixty species are known from southern Africa (i.e. Angola, Zambia, Malawi, Namibia, Zimbabwe, Botswana, Swaziland, Lesotho and South Africa) (Middleton, 2003; Kaczmarek and Michalczyk, 2004; Kaczmarek et al., 2006; Meyer and Hinton, 2009), while 37 species from 13 genera have been recorded from South Africa (Meyer and Hinton, 2009). The most recent species described from South Africa was *Minibiotus harrylewisi* (Meyer and Hinton, 2009).

3.6.2. Sampling and identification

Commonly used collection techniques includes collecting moss or lichen in paper bags, then soaking it in water for a few hours, thereafter observing the water under a microscope. Specimens are mounted on microscope slides using Hoyer's medium, and identified under high magnification. Eggs are important for the identification of species.

As far as we are aware there is no local tardigrade taxonomist and such expertise is desperately needed to explore this poorly known phylum in South Africa. The website *Tardigrada Newsletter* (http://www.tardigrada.net/newsletter/index.htm) is an excellent general source of information and contact details for tardigradologists elsewhere in the world. The use of molecular tools is opening new possibilities of research areas exploring the biogeography of this group (Czechowski et al., 2012).

3.7. Gastropoda

The Mollusca of terrestrial environments include only members of the Class Gastropoda, the familiar slugs and snails, characterised by the ubiquitous foot on which they crawl and, in the case of snails, their helically coiled shell. Within this group we find firstly the typical land snails and slugs, the Stylommatophora, that lack an operculum and possess two pairs of tentacles, the upper pair with eyes at the tip, and secondly the operculate snails with a door-like disc that closes off the shell aperture, but only a single pair of tentacles with eyes at their base. These terrestrial molluscs form a conspicuous and significant component of the soil biota. The majority are epedaphic rather than euedaphic (soil-dwelling), living and feeding in the loose surface earth and leaf-litter, rather than within the soil itself. Although there are arboreal species, particularly some members of the families Cerastidae, Charopidae, Pomatiidae and Urocylidae, which spend much of their active life on tree trunks and amongst the foliage, even these probably rely on the shelter of the soil to lay their eggs. A few, however, may be largely euedaphic appearing at the surface only when the soil is waterlogged.

The spectrum of size and morphological diversity is considerable, adult dimensions range from as little as 1 mm to well over 200 mm. Shell morphology varies greatly from species with slender awl-shaped shells to those with almost flat, discoidal shells, as well as slugs lacking an external shell or with no shell at all. In total, over 525 indigenous species (in 24 families) occur in South Africa, of which perhaps 80% are national endemics (Herbert, 1998; Herbert and Kilburn, 2004). Globally, the number of described species is estimated to be ca. 24,500 (Lydeard et al., 2004; Rosenberg, 2014). Gastropods may be found in all of South Africa's biomes, including those of the arid Northern Cape, but they are most numerous and most diverse in mesic environments, particularly where soil calcium levels are high.

Commonly, terrestrial molluscs are herbivores and detritivores, consuming a wide variety of food resources. Within the soil environment they frequently play a saprophytic role, feeding on dead and decomposing plant material thus contributing to the fragmentation of organic matter and the recycling of nutrients within the soil ecosystem. In addition, a perhaps surprising number are obligate carnivores, feeding exclusively on animal material. Some of these are generalist carnivores, preying on other snails, earthworms and probably soft-bodied soil invertebrates in general, but others are specialists with a more restricted diet, such as some of the hunter slugs (*Chlamydephorus*) that are adapted to feed on pill millipedes. Within South Africa approximately 32% of the terrestrial mollusc fauna belongs to the carnivorous families Rhytididae and Streptaxidae, the latter being a spectacularly diverse family with over 135 valid species recorded in South Africa alone and with still more awaiting description.

3.7.1. Taxonomy and collections

Description of the South African land mollusc fauna began in earnest during the 1840s and 50s, as a result of the activities of the early explorer naturalists such as F. Krauss and J.A. Wahlberg, and peaked in the 1890s and 1900s (114 and 71 species per respective decade), when resident naturalists began to take an interest in the local invertebrate biota, sending specimens to European malacologists for them to study. Subsequently species descriptions remained at a relatively high level (ca. 50 species per decade) through to the 1930s, culminating in M. Connolly's *Monographic survey of South African non-marine Mollusca* (Connolly, 1939). Since then, resident malacologists (A.C. van Bruggen, M.L. Cole, D.G. Herbert and W.F. Sirgel) have played a more significant role, but the earlier activity had clearly discovered much of the diversity and subsequent levels of species description have seldom exceeded 10 species per decade.

Even today, Connolly's monograph is the only comprehensive work on the local land snail fauna, but its utility is compromised by the limited number and often poor quality of the illustrations and of course it is now woefully out of date. There are, however, more modern and easier to use texts dealing with specific areas and aspects of the regional terrestrial malacofauna, namely Herbert and Kilburn's *Field Guide to the Land Snails and Slugs of Eastern South Africa* (Herbert and Kilburn, 2004) and a comprehensive study of *The Introduced Terrestrial Molluscan Fauna of South Africa* (Herbert, 2010).

To date the study of South Africa's indigenous terrestrial molluscs has focussed primarily on taxonomy, systematics and biogeography. Such work has traditionally utilised morphological characters of the shell, radula and distal genitalia, but more recent studies have employed an integrative approach including molecular data as well as behavioural, ecological and environmental perspectives that provide enhanced biogeographical insight and clarify conservation priorities (Herbert and Mitchell, 2009; Moussalli et al., 2009; Herbert and Moussalli, 2010; Barker et al., 2013). In most cases, however, our knowledge of the biology and ecology of the local fauna is very limited, particularly the role that the various components play in the broader ecology of the systems in which they live.

The largest collection of terrestrial molluscs in South Africa is that of the KwaZulu–Natal Museum, which now also includes collections formerly held by the Ditsong National Museum of Natural History and Albany Museum, making it the largest collection of South African land snails in the world (17,800 lots). Further important collections are present in the East London Museum (still active) and the South African Museum (dormant). Currently there are three malacologists employed at South African museums (one at the East London Museum and two at the KwaZulu–Natal Museum). Internationally, there are no scientists whose research specifically targets the South African land mollusc fauna, though representative species from South Africa are not infrequently included in broader phylogenetic studies, particularly molecular studies investigating the relationships between higher stylommatophoran taxa.

3.7.2. Sampling and identification

Terrestrial molluscs lend themselves well to invertebrate biodiversity assessments and have potential to serve as environmental indicators. Significant attributes in this regard are that: (i) the group as a whole is almost ubiquitous, but the species composition of local molluscan faunal assemblages varies considerably across the landscape; (ii) the practicalities of sampling are feasible and the scale of the task is tractable (tens rather than hundreds of species per locality); (iii) given appropriate tools, the majority of snails and slugs can be identified to species, in the case of snails, often using only shell characters; (iv) since empty snail shells remain in the environment for some time after death, a reliable indication of local faunal richness can be gained through post-mortem sampling, which is to some extent independent of seasonality (obviously not applicable to slugs).

Sampling of the regional land snail biota has largely been qualitative rather than quantitative, involving direct searching *in situ* and the collection of leaf-litter samples for subsequent sieving and scrutiny in the laboratory. Passive methods such as pitfall traps are generally not effective, although baited traps can be useful for pest species. Quantitative methods have been employed more recently, using standard area plots (20×20 m), timed searching and fixed quantity litter samples, but the application of such standard replicate methods in comparative diversity analysis across habitats with widely differing levels of molluscan abundance and diversity has been questioned (Liew et al., 2008). Although the qualitative approach has served well in documenting terrestrial mollusc diversity, as with other groups there remain gaps in the coverage and artefacts of sampling related to collecting bias. Thus the drier and more remote parts of the country have been somewhat neglected whilst regions close to towns with natural history museums (e.g. Cape Town, East London, Grahamstown, Pietermaritzburg, Port Elizabeth and Pretoria) are often disproportionately well collected and as a result appear as areas of high species richness.

3.7.3. Invasive species

As of 2010, 34 introduced terrestrial mollusc species had been recorded from South Africa, of which 28 are established and 13 invasive (Herbert, 2010). Already this figure is out of date with at least four further introductions having been identified (e.g. Rowson et al., 2016) and in all probability such introductions will continue. Noteworthy is the fact that where terrestrial molluscs are considered agricultural and horticultural pests, it is usually these alien species that are implicated rather than the indigenous

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species. In South Africa, slugs of the genera *Milax* and *Deroceras* are common agricultural pests residing in the soil.

The identification of newly discovered introductions is often difficult on purely morphological grounds, particularly if the region of origin is not known. In this regard, DNA barcoding has potential to rapidly and accurately identify new introductions, thus facilitating pest risk assessment and management. Currently, however, the reference barcode dataset for 'travelling snails and slugs' is not sufficiently representative to make this a genuinely reliable tool.

3.7.4. Future research

Although our knowledge of the diversity of terrestrial molluscs in South Africa may be considered to be good, significant knowledge gaps remain. Ongoing survey work, particularly in poorly collected areas, continues to bring to light undescribed species and more detailed study of the described taxa often results in the discovery of cryptic species. Frequently these are narrowly endemic taxa of conservation concern and biogeographic interest. Much thus remains to be discovered and clarified from a taxonomic perspective and monographic revisionary studies continue to be a research priority.

In terms of soil ecosystems, our understanding of the role that terrestrial molluscs play in the functioning of these systems in a South African context is extremely limited. In reality we can make little more than speculative remarks about their presumed role, based on their diet and what is known of other regions, although this knowledge is also limited. Therefore, quantitative research investigating molluscs as agents of decomposition, as predators of other soil organisms and as invasive species with potential ecosystem impacts would be valuable.

3.8. Isopoda

The Isopoda are one of the few crustacean orders that are diverse and well represented in marine, freshwater and terrestrial ecosystems. There are about 4500 marine, 500 freshwater and 3600 terrestrial species currently described globally. Here, we deal only with truly terrestrial isopods, which are commonly referred to as woodlice, sowbugs or pillbugs. Air-breathing species confined to the marine littoral zone (e.g. the genera *Ligia* and *Deto*) are thus excluded, although included in some previous regional reviews of 'terrestrial' isopoda (Barnard, 1932). Most terrestrial isopods are residents of decaying wood and leaf litter, where they can be very abundant, although some are obligate symbionts in termite nests. They are generally confined to damp habitats and are mainly active at night, or in wet weather. Terrestrial isopods feed mainly on leaf litter and detritus and can be important decomposers, for example in domestic compost heaps. Development is direct, with large eggs being retained in a brood pouch, or marsupium, until the young are able to fend for themselves. Longevity is usually about two years. The systematic arrangement used here follows that of Schmalfus (2003).

Despite the diversity of the fauna and importance of the group as decomposers, almost no work has been done on woodlice as decomposers within South Africa, although the significance of littoral marine species as decomposers of kelp wrack has been fairly well studied (Koop and Field, 1980, 1981). Some research has been done on their reproductive biology (Dangerfield and Telford, 1990, 1994, 1995), but almost none on their biology (with the exception of the thermal biology of the introduced species *Porcellio scaber*, Stevens et al., 2010). However, a series of studies on the biology of woodlice from Botswana and Zimbabwe have been undertaken, and these species also occur in South Africa. The reproductive biology of the introduced *Porcellionides pruinosus* is documented by Dangerfield and Telford (1990), while further information on population structure and sex ratios of several species are given by Dangerfield and Telford (1994, 1995) and of partial brood release mechanisms by Telford and Dangerfield (1994). Telford and Dangerfield (1995) also document size variations in the offspring of six species of woodlice.

3.8.1. Taxonomy and collections

The South African isopod fauna is a diverse one and has been reasonably documented in the taxonomic literature. The marine component of the fauna was last fully described by Kensley (1978) who listed 275 species, including a few from outside the political borders of South Africa. The freshwater fauna was also described by Kensley (2001) and comprises 18 species (one of which is in fact exclusively estuarine). The last comprehensive listing of the terrestrial Isopoda of the southern African region was that of Barnard (1932), who listed 145 species, but 10 of these were confined to the seashore and are thus not fully terrestrial, while more than 20 others were not reported from within South Africa itself. To these need to be added five new species reported by Taiti and Ferrara (1982) and 10 of the 14 species reported from the wider southern African region by Ferrara and Taiti (1985). The current known terrestrial isopod fauna thus includes 127 species (Picker and Griffiths, 2011). The major regional collections are those in the Iziko South African Museum in Cape Town, and that of the KwaZulu–Natal Museum in Pietermaritzburg.

3.8.2. Sampling and identification

Woodlice are easily collected using pit-fall traps or by hand. There are no taxonomists in the region currently working on isopods from any habitat and both the marine and terrestrial guides are in dire need of revision. Little or no ecological research is currently underway.

3.8.3. Invasive species

Introduced species can be extremely abundant in urban areas, but their distribution patterns remain very poorly known, as sampling has tended to focus on natural habitats, rather than disturbed ones. Of the 127 known South African terrestrial isopod species, six are introduced (Picker and Griffiths, 2011).

3.8.4. Future research

There is no question that total terrestrial isopod species richness is currently underestimated. All authors to date have reported high proportions of new species in the collections they examined and no work has been done on the systematics of the group for more than 25 years. Distribution patterns are also poorly known and many of the species in the current fauna are reported from one or a handful of localities. This often reflects poor sample coverage, but may, in some cases, indicate that some species are indeed very restricted in habitat and may possibly be threatened. This needs to be resolved. Key topics for future research include additional taxonomic surveys and descriptions, determining the extent to which introduced species have penetrated into untransformed habitat and whether they have displaced, or are competing with, the diverse indigenous fauna, as well as the role of both introduced and indigenous species as decomposers.

3.9. Amphipoda

Amphipods are primarily a marine group, although some occur in freshwater (reviewed by Griffiths and Stewart, 2001) and a single family, the Talitridae, has become air-breathing and has successfully colonised terrestrial habitats. The majority of talitrids are either burrowing forms that are confined to the intertidal and supralittoral zones of sandy beaches, or non-burrowing species associated with algae on rocky and sandy seashores. These groups are conventionally referred to as 'sandhoppers' and 'beachfleas' respectively (Friend and Richardson, 1986) and the regional species are listed by Griffiths (1976). South African sandhoppers have been relatively well studied, both in terms of their population dynamics (Van Senus, 1988; Van Senus and McLachlan, 1989) and their effectiveness as decomposers (Griffiths et al., 1983; Stenton-Dozey and Griffiths, 1983). However, as they are essentially a marine group, they are not considered further here. This account is rather focused on the truly terrestrial 'landhoppers' that live primarily in forest litter, independent of water bodies. Landhoppers are primarily nocturnal, cryptic residents of the forest floor and are found mostly in the southern hemisphere and tropics, feeding on angiosperm leaves and detritus (Friend and Richardson, 1986). Most are local endemics, although a few have become widely distributed by man; indeed some so-called 'tramp' species are so widespread that it is now impossible to trace their origins (Bousefield, 1984).

3.9.1. Taxonomy and collections

The history of discovery and current taxonomic status of the South African landhopper fauna has been comprehensively reviewed by Griffiths (1999), so this is not repeated here. The currently recognised fauna comprises seven species, five of which are members of the endemic genus *Talitriator* and two of which are introduced forms belonging to the widely dispersed genus *Talitroides*. Almost all the existing regional collections are located in the Iziko South African Museum in Cape Town, with small additional collections in the KwaZulu–Natal Museum and Ditsong National Museum of Natural History.

3.9.2. Sampling and identification

Landhoppers are relatively easy to collect using pit-fall traps, soil extraction funnels or by using a hand net, although as they are active jumpers, quantitative sampling is difficult. The regional species are all well described and illustrated by Griffiths (1999), so can be readily identified to species, although some practice is needed to observe the identifying characters.

3.9.3. Invasive species

The situation with regard to introduced species is very different in that both known introduced taxa are reported from only two isolated records and their current distribution remains unknown. It is in fact highly likely that both species in reality occur in irrigated urban gardens throughout the region, as they are commonly dispersed with nursery plants. They can also become very abundant, but landhopper 'invasions' into suburban homes are of minor concern.

3.9.4. Future research

Endemic landhoppers are a common component of the cryptic fauna of forests throughout the moister regions of South Africa, stretching in a wide swathe from the Cederberg in the Western Cape to the Zimbabwe border in the North-East (Griffiths, 1999), but we are not aware of any papers that specifically examine their biology or ecological role within this region. The endemic fauna is relatively well known and it seems unlikely that many species remain undiscovered, or that the distributions patterns mapped by Griffiths (1999) will be substantially revised.

There are no local publications about the adaptations, life history or ecological roles of South African landhoppers, although there is a substantial international literature as reviewed by Friend and Richardson (1986). Almost all known species are restricted to high humidity habitats and have a 1–2 year life-cycle, although reproduction can be seasonal, or occur year round. The diet consists of leaf litter and although population densities can run into thousands of individuals per m^2, landhoppers do not appear to ingest a high proportion of the litter fall, populations probably being restricted by climatic factors rather than food availability. Landhoppers can, however, be a significant food resource for predators, mainly birds and Australian marsupials (Friend and Richardson, 1986). Priorities for future research in South Africa include mapping the distribution patterns of the two introduced species, determining whether they have spread into untransformed habitats, and if so, whether they compete with or eliminate the local indigenous species.

3.10. Myriapoda

Myriapods are often a conspicuous component of leaf litter and soil habitats in all South African biomes. Members of the subphylum are characterised by a body divided into a head and segmented trunk, one or two pairs of legs on most body segments, and a single pair of antennae. The subphylum comprises four classes, namely the Diplopoda (millipedes), which have an estimated global richness of over 80,000 species (although just over 12,000 have been described), Chilopoda (centipedes), with about 3000 known species globally and two less diverse and small-bodied groups, the Pauropoda and Symphyla (each with fewer than 500 species globally). The millipedes, pauropods and symphylans are all detritivores which feed mostly on decomposing organic matter, while the centipedes are predators, although one order, the Geophilomorpha, also have saprophytic tendencies.

Millipedes are represented by seven orders and 15 families and centipedes by four orders and 12 families in South Africa. The fauna has been sporadically studied since the description of the first three South African millipede species by Brandt (1841) and the first centipede species in the late 1700s. The first comprehensive taxonomic review of South African Myriapoda was that of Attems (1928) of the Natural History Museum of Vienna, who based his publication on an examination of the entire South African Museum myriapod collection.

3.10.1. Diplopoda

Attems (1928) included 65 known millipede species and an additional 111 new species, some of which were from neighbouring countries, in his major work on southern African myriapods. Later R.F. Lawrence of the KwaZulu-Natal Museum was the first locally based taxonomist to research South Africa's millipedes and he described a total of 91 species between 1938 and 1973 (Lawrence, 1953b, 1958, 1962, 1963, 1967b, 1969, 1970). In 1998 a checklist of the southern African fauna was published (Hamer, 1998). Since then most research has focussed on the order Spirostreptida and an additional 23 new species have been described (Hamer, 1999, 2000, 2009; Mwabvu et al., 2009; Redman et al., 2003). A single publication reviewed some of the Sphaerotheriida (*Sphaerotherium)* (pill millipede) species (Van der Spiegel et al., 2002) and this research highlighted the many taxonomic problems in the group. The other two main orders of millipedes, namely the Polydesmida (keeled millipedes) and Spirobolida have not received any real attention for almost 50 years and they, and the Sphaerotheriida, need taxonomic review. The other three millipede orders have few species recorded, and include small-bodied, obscure millipedes such as the sucking millipedes (Siphonophorida and Polyzoniida), and the pincushion or bristly millipedes (Polyxeniida). The actual diversity in these taxa is not well known because they are seldom collected. There has, however, been some research on these taxa with a redescription of a siphonophorid (Shelley and Hoffman, 2004) and the description of two new polyxenid species from Table Mountain (Nguyen Duy-Jacquemin et al., 2011).

The estimated millipede diversity in South Africa is approximately twice the known richness of 467 species (Fig. 5, Hamer and

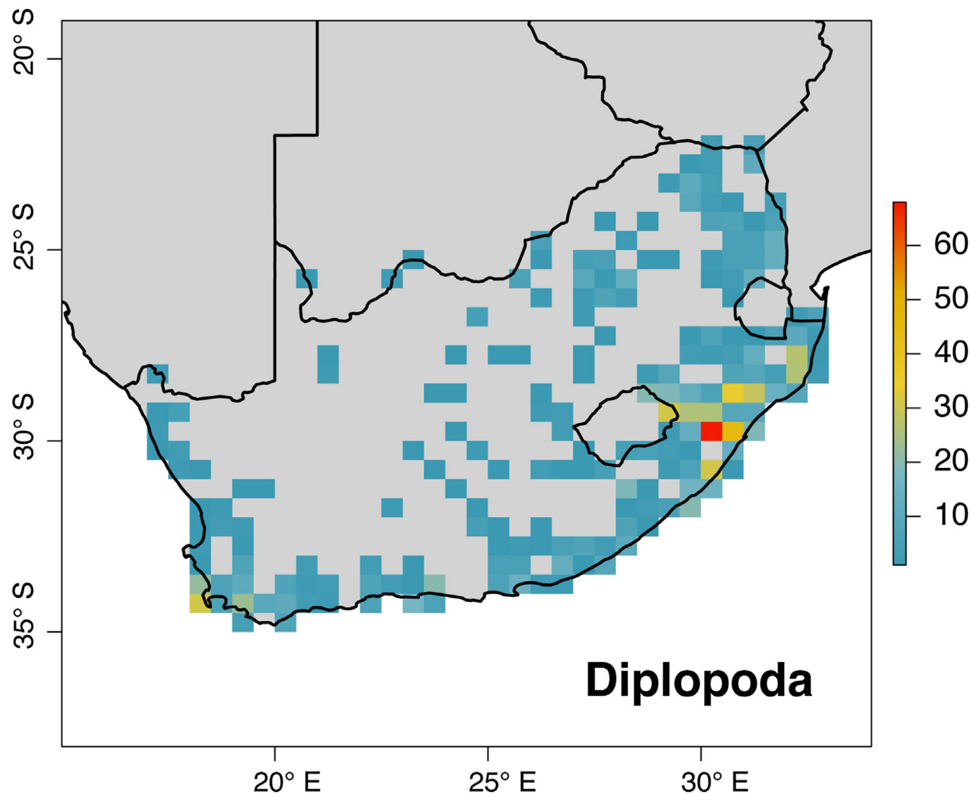

Fig. 5. Species richness distribution for millipedes in South Africa.

Slotow, 2002). This estimate is based on several surveys of forest (Hamer and Slotow, 2009), grassland (Hamer and Slotow, 2009) and savannah (Hamer et al., 2006), where the proportion of undescribed species has ranged from 44–57%.

The main South African millipede collections are those of the KwaZulu–Natal Museum in Pietermaritzburg where the bulk of Lawrence's material is housed (200 type lots, 1600 other lots), and the Iziko South African Museum whose collection includes much of the old material that was examined by Attems (500–600 lots of types and about 2000 other lots). Many of the samples examined by Attems are missing gonopods, which may be in the Vienna Museum of Natural History where Attems was based. Smaller collections are held by the Ditsong National Museum of Natural History (858 lots) and the National Museum in Bloemfontein (116 lots). The Lundt Expedition material is still housed at the Lundt University in Sweden, and various other European and United States institutions have some material from South Africa but details of these collections are lacking. The same South African institutions are likely to also house the largest centipede collections but no details have been compiled.

3.10.2. Chilopoda

Most of the centipede species from South Africa were described in the nineteenth and early twentieth century. The number of species has only increased slightly since Attems (1928), with a further 32 species described by Lawrence (1955a) in the *South African Animal Life* review and his subsequent smaller papers (Lawrence, 1958, 1959, 1963, 1967a, 1968). Only one new species of centipede has been described from South Africa in the last 40 years (Edgecombe, 2003) but this is likely to be a result of the absence of a resident taxonomist and little focussed sampling or taxonomic research on the fauna. A total of 113 species and subspecies are currently known from South Africa, although it is unlikely that the centipede fauna is anywhere near as diverse as the millipede fauna. This is based on the fact that many of the centipede species, especially those in the Scoplopendromorpha, appear to be relatively widespread, and the much lower global diversity of centipedes. The Geophilomorpha are the most diverse centipede order both globally and in South Africa. Most of the undiscovered diversity is likely to be in this order as they are usually in deeper soils and so are not well sampled or studied. Studies on molecular diversity may, however, reveal much more diversity than is currently identifiable based on morphology and this aspect of the South African fauna requires investigation.

3.10.3. Pauropoda and Symphyla

The Pauropoda and Symphyla of South Africa have never been studied in any detail, and only four species of each group are currently known (Scheller, 1979). Even globally, knowledge of the diversity of these taxa is very poor and most of the taxonomic work over the last 50 years has been published by a single taxonomist.

3.10.4. Sampling and identification

In depth analyses of sampling methods for millipedes and centipedes have been published from two different studies in South African savannah. Druce et al. (2004) found that active searching of quadrats was more effective and efficient than passive methods such as pitfall trapping and baited traps for both millipedes and centipedes. The results in forest were similar (Uys et al., 2010). An extensive survey of various invertebrate taxa including millipedes and centipedes in Mkhuze and Phinda Game Reserves in KwaZulu–Natal showed that after sampling more than 80 one hectare sites, with active and intense searching of two 10×2 m quadrats with no time limit and active searching of two 20×20 m plots for a total of an hour in each site, at least 80% of the millipede and centipede faunas of the area had been sampled. Lovell et al. (2010) recommended the intense searching of the

2 × 10 m quadrat as a sampling method because although it is more time consuming, it did provide more species than random or plot searches that covered a larger area but had a time constraint. Active searching has the additional benefit of allowing preliminary sorting in the field, which means that the impact on the fauna is reduced as a large number of duplicate specimens can be released once they have been recorded, and there is no by-catch inadvertently killed. This is especially important for relatively long-lived taxa of conservation concern such as many of the large millipedes and centipedes which may take three or more years to mature and live for between five and eight years.

Any sampling strategy for millipedes needs to take into consideration seasonal patterns of activity (Hamer et al., 2006; Uys et al., 2010). Millipedes are generally active during the wet season, especially in terms of surface activity. During the dry months it seems that many species are dormant deep in the soil, emerging only after rains.

There is one part-time taxonomist who has some expertise in identification across most millipede orders (M. Hamer, SANBI) and one expert on the Spirostreptidae who is actively publishing (T. Mwabvu, University of KwaZulu–Natal). Internationally there are no experts focussing on the millipede taxa of South Africa. Given the predicted number of undescribed species, the large gaps in survey data, and the importance of millipedes in terms of endemism and thus conservation value and their role in soil fertility, there is certainly scope for more specialists. There is currently no expert capacity within South Africa for centipede taxonomy and identification.

There are no comprehensive identification guides to species level for South African myriapods and currently identification requires access to a range of taxonomic publications that deal with family or genus level treatments or that include descriptions of various myriapod species. Identification of most millipedes requires examination of the gonopods of mature male specimens and this can be challenging for non-experts, but a well-illustrated guide would be extremely useful and should be considered as a priority gap for future efforts. Useful resources for millipedes, including a list of all genera, the list of millipede collections, and links to various publications and are available on the *MILLI-PEET* project website (http://archive.fieldmuseum.org/millipeet/), and a searchable database of all centipede species is available at http://chilobase.bio.unipd.it/. DNA barcoding for myriapods has been initiated in Europe and Taiwan but not in South Africa.

3.10.5. Invasive species

Seven alien millipede species have been recorded in South Africa, but these are generally limited in distribution, with the exceptions of invasions in the Western Cape by several species of Mediterranean origin. Surveys of natural habitats in many parts of South Africa have not revealed alien millipede species, even where there are abundant invasive earthworm populations. No alien centipedes have been formally recorded in South Africa, but it is difficult to be certain about this until the taxonomy is improved. One species of house centipede (*Scutigera coleoptrata*) is considered to be of Mediterranean origin and to have been introduced almost globally, including to South Africa.

3.10.6. Future research

Apart from the taxonomic research which is required, much of South Africa remains unsurveyed for myriapods. The high levels of endemism in millipedes, and the previous focus on forests, means that existing knowledge of diversity and biogeography is far from complete. However, the economic rationale for gathering this type of information is unclear as the value of millipede diversity relative to soil nutrient and decomposition cycles in agricultural and natural ecosystems has not been quantified (see Heemsbergen et al., 2004). In addition, future surveys must be quantified to allow comparisons of both richness and density, and to provide baseline data for future monitoring and measurement of impacts of habitat and climate change.

3.11. Araneae

Spiders are a prominent component of the soil and leaf litter fauna in all terrestrial ecosystems, and are well represented in all of the South African biomes. The order is divided into three suborders, Liphistiomorphae, Mygalomorphae and Araneomorphae, of which the latter two are represented in South Africa. Spiders can be separated from other arachnids by the presence of spinnerets ventrally at the end of the abdomen that are used to produce various types of silk, as well as the fangs situated on the chelicerae that are used to inject venom to immobilise prey.

Spiders are the sixth most species rich order of arthropods (Zhang, 2011), with more than 46,000 species described globally (World Spider Catalogue, 2016), of which only an estimated one-third (Agnarsson et al., 2013) to half (Platnick and Raven, 2013) of the global diversity has been described. Dippenaar-Schoeman et al. (2010) reported 2003 species from South Africa, although this figure has since risen to 2170 species from 73 families through taxonomic revisions and species descriptions (Dippenaar-Schoeman et al., 2015). A high proportion of these species (59.3%) are endemic to the country (Dippenaar-Schoeman et al., 2015), although this may be influenced by low inventory levels beyond South Africa's borders (Foord et al., 2011; Jocqué et al., 2013). Of the known South African species, 1331 (62%) are associated with the soil surface.

All species of spiders are predacious in all of their life stages, and thus play an important role in terrestrial ecosystems as predators of other invertebrates, particularly insects and mites (Dippenaar-Schoeman et al., 2013a,b). Depending on the taxon concerned, spiders may build a silk web structure to capture prey, while others actively hunt their prey or wait in ambush for passing prey (Cardoso et al., 2011). Spiders play an important role in soil food webs, and are often the dominant predatory group in the soil macrofauna (e.g. Burgess et al., 1999; Doblas-Miranda et al., 2007, 2009). In litter habitats, their predation on detritivores (e.g. Collembola) may affect the rates of litter decomposition (Lawrence and Wise, 2000, 2004).

3.11.1. Taxonomy and collections

The taxonomic descriptions of South African spiders reached a first peak during the late 1800s and early 1900s, when more than 730 species were described (Fig. 2). From the late 1910s, two South African arachnologists, Tucker (1917, 1920, 1923) and Lawrence (1937, 1938a, 1940, 1942, 1947, 1952, 1964) produced many significant papers, the latter continuing to publish on spiders until 1980 (Lawrence et al., 1980). During the last two decades, there has been a second peak, and since 1980 more than 500 species have been described due to modern taxonomic revisions and the development of several South African taxonomists that have delivered sizable inputs. Of particular mention here are A. Dippenaar-Schoeman, C. Griswold, R. Jocqué, W. Wesołowska, L. Lotz, R. Lyle, C. Haddad and B. Huber, who together have contributed descriptions of more than 430 species from South Africa alone. In part, the increase in taxonomic study of the fauna since 1997 can be attributed to the establishment of the South African National Survey of Arachnida (SANSA), and partly due to international networking and collaboration (Dippenaar-Schoeman and Jocqué, 1997), which resulted in a renewed interest in spider taxonomy in South Africa.

Considering the drastic increase in the number of records sampled during the last decade (Fig. 2) and the poor taxonomic

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resolution of several families in South Africa (e.g. Agelenidae, Clubionidae, Theridiidae, Linyphiidae, and Lycosidae, and most of the mygalomorph spiders), it is likely that a large number of new species will be described from the country in the future.

Aside from the South African collections that house a large number of specimens (Supplementary material S1), several international institutions house sizeable collections of material from the country. Most notable are the Museum National d'Histoire Naturelle (Paris, France), where types of many species described by Simon are deposited, as well as the Royal Museum for Central Africa (Tervuren, Belgium), California Academy of Sciences (San Francisco, U.S.A.), and Natural History Museum (London, U.K.), amongst others. For detailed information on collections of importance in arachnological research see Supplementary Material S1.

3.11.2. Sampling and identification

Historically, sampling of ground- and soil-dwelling spiders in South Africa was largely dependent on pitfall trapping and less on litter sifting, hand collecting and Tullgren funnels or Winkler bags. However, the more extensive use of methods to sample in leaf litter, during the last decade particularly, has gone a long way to discovering cryptic macro- and mesofauna components that are very rarely collected using pitfalls. Their future use in all surveys should be strongly encouraged.

South Africa has several spider experts. Dippenaar-Schoeman and R. Lyle are based at the National Collection of Arachnida, Agricultural Research Council. Dippenaar-Schoeman is a world expert on Thomisidae and has also worked on several other families, including the Ammoxenidae and Eresidae, and is regarded as the researcher having the broadest knowledge of African spider taxonomy. She is now assisted by R. Lyle, who has in the past worked on Trachelidae and is now involved in research on Idiopidae trapdoor spiders. At the National Museum in Bloemfontein, L. Lotz specialises on the taxonomy of archaeid, miturgid and sicariid spiders. Foord (University of Venda) is a specialist on Afrotropical Hersiliidae, while C. Haddad (University of the Free State) is a specialist of Corinnidae, Gallieniellidae and Salticidae spiders.

Aside from taxonomic literature, several resources are now available to facilitate the identification of South African spiders, including several textbooks (Dippenaar-Schoeman and Jocqué, 1997; Dippenaar-Schoeman, 2002; Holm and Dippenaar-Schoeman, 2010), field guides (Dippenaar-Schoeman and Van den Berg, 2010; Dippenaar-Schoeman et al., 2013a,b; Dippenaar-Schoeman, 2014; Dippenaar-Schoeman and Haddad, 2014), the *First Atlas of South African Spiders* (Dippenaar-Schoeman et al., 2010), and websites such as the SANSA Virtual Museum (www.arc.agric.za:8080) and the African Arachnida Database (www.arc.agric.za:8081).

3.11.3. Invasive species

Little is known about invasive spiders in South Africa. Some of the invasive species are discussed in the *First Atlas of South African Spiders* (Dippenaar-Schoeman et al., 2010) and a book on invasive arthropods in South Africa (Dippenaar-Schoeman et al., 2011). In a recent review of spiders of the Grassland Biome, 38 of the 792 species recorded were considered to be introduced or cosmopolitan (Haddad et al., 2013). Most of these species are web-dwellers and plant wanderers, and mainly occur in synanthropic environments.

3.11.4. Future research

The inabilities to not only identify South African, but also Afrotropical spiders, remains the single greatest hurdle hindering more applied research on the continent. Although the SANSA project has enabled considerable advances to be made to spider taxonomy and ecological research, there are still strong biases in the distribution of species data in the country (Fig. 6). Large parts of

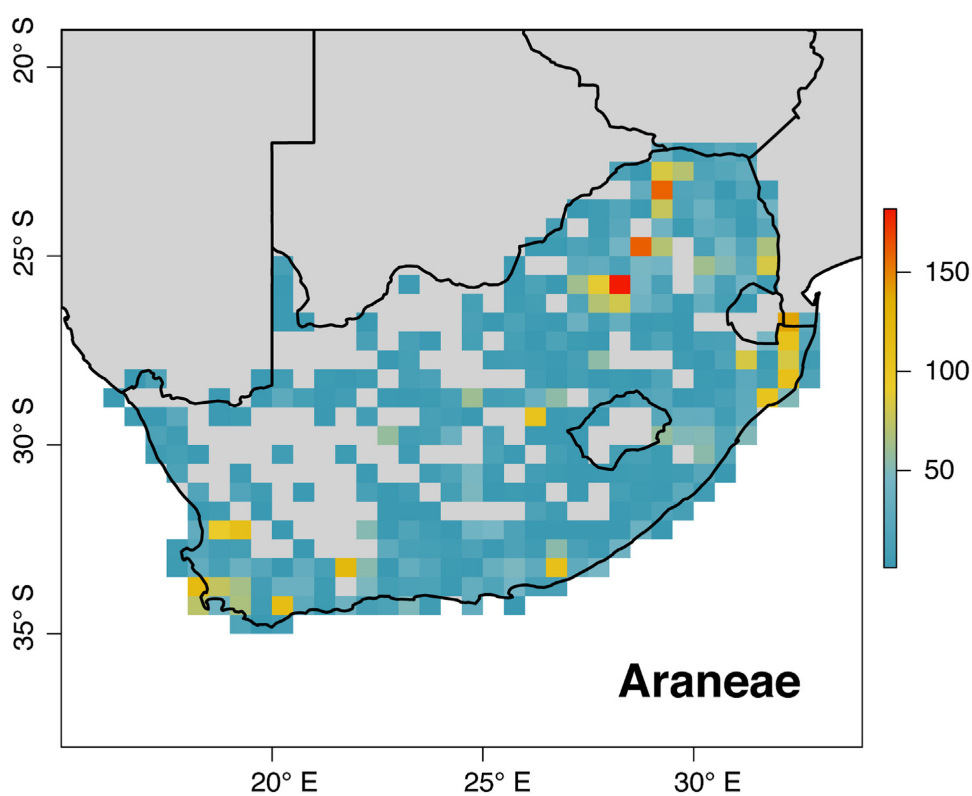

Fig. 6. Species richness distribution for spiders in South Africa.

the North West, Northern Cape and Eastern Cape Provinces still need to be sampled, which has led to a substantial underestimation of the species diversity of certain biomes (i.e. the Nama Karoo, Thicket and Succulent Karoo Biomes are likely undersampled). Even in the comparatively well sampled Grassland and Savannah Biomes, many areas are poorly sampled and could benefit from more intensive surveys. Without this sampling as a basis, making accurate conservation assessments and hypotheses of the patterns affecting spider diversity will remain a challenge. The implementation of a standardised sampling protocol for the SANSA project (carried out in more than 40 degree-squares between 2007 and 2014) and its future use will go a long way to generate data to better understand the distribution of spider species in the country.

Although Red Listing assessments are currently underway for all spiders, further sampling and identification of material can pave the way for more accurate conservation assessments covering a broader range of taxa in the future.

3.12. Opiliones

Though part of the class Arachnida, harvestmen form an order on their own, the Opiliones. They seem to be closely related to scorpions (order Scorpiones), pseudoscorpions (order Pseudoscorpiones) and solifuges (order Solifugae), but their exact placement in the Arachnida is not yet clear (Pinto-Da-Rocha et al., 2007). Their cephalothorax and abdomen are broadly joined together, though still discernable as separate body parts. Because they mostly have long legs, they are often confused with spiders, but they do not have venom glands or spinning organs. Unlike spiders, they have a relatively limited habitat preference, being found mostly in damp or humid habitats, such as forests, caves or the coastal mist-belt. In South Africa this forms the typical distribution, from the Cape Peninsula up along the south and eastern coasts into Mozambique, with only a few species found in the more atypical dryer western areas.

Opiliones mostly live close to the ground in the leaf litter, though some may also live higher up in vegetation and trees and some live in caves. Like most Arachnida, opilionids are mostly carnivorous, but some are omnivorous and will eat plant matter and fruit. Some will also scavenge and eat dead plant matter and animals.

3.12.1. Taxonomy and collections

The distribution of Opiliones, as reviewed here, is chiefly based on the work of Kauri (1961), Lawrence (1931, 1938b), Staręga (1984, 1992), Boyer and Giribet (2007), Hunt and Cokendolpher (1991), Kury (2003, 2006), Pinto-Da-Rocha et al. (2007) and Lotz (2009, 2011).

Of the approximately 6400 Opiliones species known to occur worldwide, about 208 occur in South Africa (192 endemic species). These species are currently grouped in three suborders, namely: the Cyphophthalmi (one family, three genera, 16 species); the Laniatores (four families, 34 genera, 150 species); and the Eupnoi (three families, five genera, 42 species).

The three genera of the suborder Cyphophthalmi (family Pettalidae) are *Speleosiro, Parapurcellia* and *Purcellia*. In the suborder Eupnoi, the small families Caddidae and Niopilionidae are represented in South Africa by only 10 species, seven in Caddidae (one genus) and three in Niopilionidae (two genera). The third family, Phalangiidae, is represented in South Africa by two genera and 32 species. The genus *Guruia* is represented by a single species and the remaining 31 species belong to the genus *Rhampsinitus*. In the suborder Laniatores four families are currently recognised in South Africa. The Assamiidae (two genera and two species), the family Biantidae (three genera, 22 species), the Triaenonychidae (28 genera and 125 species) and the family Trionyxellidae (one genus and one species).

3.12.2. Sampling and identification

Opiliones are mainly sampled by means of hand collecting, leaf-litter sifting and pitfall traps. Though pitfall traps can deliver large amounts of specimens, hand collecting and leaf litter sifting deliver more species.

Identification of South African Opiliones is mainly done with keys by Kauri (1961), in combination with Lawrence (1931, 1938b), Staręga (1984, 1992), Boyer and Giribet (2007), Hunt and Cokendolpher (1991), Kury (2003, 2006), Pinto-Da-Rocha et al. (2007) and Lotz (2009, 2011). Unfortunately, the most species-rich genera are those most in need of taxonomic revision to facilitate proper identification.

3.12.3. Future research

South Africa is in need of taxonomists and revisions of the major Opiliones genera. Also, many sampling gaps exist, and as some species are only known from the type specimen/s, there is a need to collect at the type localities.

3.13. Scorpiones

Scorpions are the fifth most diverse arachnid order in number of described species, with more than 2 000 extant species in approximately 180 genera and 18 families (Prendini, 2011a,b). Three families, ten genera and 101 species are recorded from South Africa based on the most recent peer-reviewed literature (Newlands and Prendini, 1997; Prendini, 2000, 2001a,b, 2004a, 2005a, 2004b, 2005b, 2006, 2015). The fauna includes six genera and 38 species of Buthidae. Hormuridae, previously referred to as Liochelidae and, before that, Ischnuridae (Monod and Prendini, 2014), contains three genera and 24 species in South Africa. *Opisthophthalmus* is the sole representative of the family Scorpionidae in South Africa and the most diverse genus in the country, represented by 39 described species. All *Opisthophthalmus* species are fossorial, excavating burrows of varying length and configuration under stones or in open ground, in soils of specific hardness, texture or composition (Prendini, 2001a,c; Prendini et al., 2003).

3.13.1. Taxonomy and collections

Prior to 1898, taxonomic work on the scorpions of southern Africa was conducted in Europe (mostly Germany, France, Sweden and the U.K.) by prominent arachnologists of the time, including A. A. Birula, C.G. Ehrenberg, F. Karsch, C.L. Koch, L. Koch, K. Kraepelin, W. Peters, R.I. Pocock, T. Thorell and E. Simon. Together they described most of the currently recognised genera and many of the species. Some continued working on the fauna into the early 1900s, and were joined by others from Europe, e.g., S. Hirst, A. Monard, A. Penther, C.F. Roewer and F. Werner. The first South African arachnologist to publish on scorpions was W.F. Purcell, whose four monographs (Purcell, 1898, 1899a,b, 1901) laid the foundations of knowledge on the South African scorpion fauna. Picking up where W.F. Purcell left off, J. Hewitt published two monographs (Hewitt, 1918, 1925) and several shorter papers until the mid-1930s. Lawrence overlapped with Hewitt in the 1920s and 1930s, and continued publishing on the scorpions (and other arachnids) of South Africa, describing various new species, until the 1980s. Lawrence's (1955b) contribution to *South African Animal Life* remained the standard reference into the 1990s. E.B. Eastwood, B. H. Lamoral, and G. Newlands worked on the fauna in the 1970s and 1980s. Most systematic work on South African scorpions since the mid-1990s was by L. Prendini, with contributions by M.J. FitzPatrick. Landmark studies on the behaviour of South African scorpions were published by A.J. Alexander from the 1950s to 1970s (e.g., Alexander, 1957, 1958, 1959, 1972). Fewer contributions have been published on the ecology of South African scorpions (e.g. Lamoral, 1971a,b; Newlands, 1972; Eastwood, 1977, 1978a,b; Foord et al., 2015).

The scorpion collections of South Africa reflect the areas where arachnologists worked. The Iziko South African Museum houses the oldest collection, whereas the Ditsong National Museum of Natural History holds the largest collection. Other important historical collections are housed at the Albany Museum and the KwaZulu–Natal Museum, while smaller but significant collections from the 1980s onwards are deposited at the National Museum and the National Collection of Arachnida, ARC-PPRI. A small but neglected historical collection with a few types exists at the McGregor Museum. Major collections of South African scorpions abroad are housed at the following institutions: American Museum of Natural History (New York, U.S.A., the largest collection outside South Africa); California Academy of Sciences (San Francisco, U.S.A.); Natural History Museum (London, U.K.); Museum National d'Histoire Naturelle (Paris, France); Museum für Naturkunde (Berlin, Germany); Royal Museum for Central Africa (Tervuren, Belgium); Zoologisches Museum, (Hamburg University, Germany).

3.13.2. Sampling and identification

Scorpions are traditionally hand collected during the day by turning stones, peeling bark, prising open rock crevices and sifting leaf litter. Fossorial scorpions may be collected by excavating burrows or by setting pitfall traps in front of burrow entrances before nightfall. Night collecting with portable ultraviolet (UV) flashlights is the preferred method for collecting scorpions (Sissom et al., 1990), especially surface-active adult males. Most scorpions fluoresce brightly under long-wave UV light. Combining UV detection, hand collecting, burrow excavation and pitfalls usually collects a greater diversity of taxa and semaphoronts (males, females and immature stages) than any single method.

Reliable identification of South African scorpions depends on expert examination or consultation of keys and descriptions in the primary taxonomic literature, e.g., Lawrence (1955b), Newlands and Cantrell (1985) and Prendini (2004a), and shall continue to do so until all genera are comprehensively revised to modern standards. 'Eyeballing' photographs and distribution maps in amateur field guides and websites, while increasingly popular, is bound to lead to misidentifications for several reasons: (i) photographs are often misidentified by self-proclaimed 'experts' and distribution maps inaccurate due to the limited understanding of species distributions, (ii) closely related species are seldom possible to separate without verifying diagnostic characters on specimens under a microscope and (iii) species identification in several genera (e.g. Hormuridae) relies on sexually dimorphic characters of adult males, in the absence of which, adult females and immatures are often impossible to identify.

3.13.3. Future research

More work is needed to determine the known diversity of South African scorpions for two reasons. Firstly, scorpions are cryptic, seasonal, habitat-specific, and difficult to collect without appropriate methods. Most habitats where they occur, especially in the arid western parts of the country, have not been surveyed in appropriate seasons, using appropriate methods, or by people experienced in collecting scorpions. Secondly, scorpion species are often difficult to delimit because, unlike many other arachnid orders, scorpion genitalia provide insufficient characters at the species level in many families, and data from DNA sequences and venoms have revealed cryptic diversity in many putative widespread polymorphic species (e.g., Dyason et al., 2002; Prendini, 2001a, 2001d; Prendini et al., 2003). Prendini has actively surveyed and revised the fauna since the mid-1990s and will continue to do so in the foreseeable future with several major generic revisions nearing publication. These efforts, which applied an integrative approach, combining data from morphology, DNA and geographical distributions, were assisted by new material collected during the past decades by the South African National Survey of Arachnida, the South African Reptile Conservation Assessment, and the local scientific community. Studies on the ecology, life history and behaviour of South African scorpions are almost non-existent and represent a fascinating area for exploration.

3.14. Pseudoscorpiones

Pre-Devonian in origin, the Pseudoscorpiones are one of the oldest extant arthropod lineages (Shear et al., 1989; Schawaller, 1991). Over the past 380 million years they have diverged into more than 3500 known extant species in 26 families (Harvey, 2013). All pseudoscorpions are predatory in nature, and based on the study of fossilised specimens from Baltic, Dominican and Mexican ambers by Shear et al. (1989), this has been the case for millions of years. Most are less than five millimetres in length, though they range from less than one millimetre in some Chthoniidae to just over ten millimetres in females of *Garypus titanius* (see Beier, 1961). They superficially resemble true scorpions, but lack the elongated metasoma (tail) and telson (sting) of their namesake (Harvey, 2002, 2007). They do, however, possess the characteristic six-segmented pedipalps with the tibia and tarsus modified into a chela with a movable finger.

3.14.1. Taxonomy and collections

Until the 1900s, only three South African pseudoscorpion species had been described (Ellingsen, 1912), namely *Cordylochernes octentoctus*, *Withius simoni* and *W. tenuimanus* (all described by Budapest Balzan and Voyage de, 1892). Historically most of the early research, specifically species descriptions, was done by foreign scientists. The works of Tullgren (1907), Ellingsen (1912) and to a lesser extent Hewitt and Godfrey (1929) saw an abundance of new species descriptions, both from field expeditions as well as examination of museum specimens. Max Beier was by far the greatest contributor to the field, describing more than half of the currently known species in the region from 1947 to 1964 (Dippenaar-Schoeman and Harvey, 2000). After 1964 the discovery of new species decreased drastically, with species described by Manhert (1988). In was only during the second half of the 20th century that researchers based in South Africa, such as Lawrence (1967c) from the KwaZulu–Natal Museum, started to publish checklists of species found within the region. Dippenaar-Schoeman and Harvey (2000) published a complete checklist and catalogue of species found within South Africa, and in subsequent years several checklists of nature reserves would follow (Haddad et al., 2006; Haddad and Dippenaar-Schoeman, 2009). South Africa currently has 135 known species and 10 subspecies in 15 families, with over 70% of these species endemic to the country (Dippenaar-Schoeman and Harvey, 2000).

Following advances in pseudoscorpion taxonomy, both morphologically (Harvey, 1992), as well as phylogenetically (Murienne et al., 2008), a decision was made to start working on taxonomic revisions of the South African pseudoscorpions, with a revision of the family Geogarypidae recently completed (Neethling, 2015).

For details on collections of importance, see Supplementary material S1 on spiders.

3.14.2. Sampling and identification

Efficient sampling of soil- and ground-dwelling pseudoscorpions relies heavily on the utilisation of leaf litter extraction methods, including litter sifting, Winkler bags and Tullgren funnels. Pitfall traps usually perform very poorly in collecting pseudoscorpions, and are not recommended for sampling this group. Particular taxa (e.g. Atemnidae and Olpiidae) are frequently collected from beneath rocks. Recently, canopy fogging and sampling from beneath bark have proven very effective to sample the arboreal fauna, while foliage beating rarely yields pseudoscorpions. This suggests that most arboreal species are closely associated with bark.

Until recently, all of the taxonomic experts on African pseudoscorpions were based overseas. The leading international experts on African pseudoscorpions include M. Harvey (Western Australian Museum, Perth), M. Judson (Museum National d'Histoire Naturelle, Paris) and V. Mahnert (Muséum d'Histoire Naturelle, Geneva). As a consequence, a large proportion of the material housed in South African collections remains unidentified. Since R.F. Lawrence, who described a few species during the last century, few South African arachnologists have done taxonomic research on local pseudoscorpions. However, a recent revision of the South African Geogarypidae (Neethling 2015) is the first contribution in an effort to develop local taxonomic expertise on pseudoscorpions.

3.14.3. Future research

Despite recent taxonomic revisions, and the work done by Murienne et al. (2008) bringing the systematic of the Pseudoscorpiones into the molecular age, detailed morphological and ecological data is still lacking for the vast majority of pseudoscorpions, including the poorly-known South African fauna. Many of the original species descriptions are no more than a single paragraph with a simple sketch. Short-term future research will focus on revisions of previously described species, the description of any new species and reducing the gaps in the largely unsampled areas in the interior of the country. Following the revisions, further research will focus on gaining ecological data, as well as incorporating South African species into global studies.

3.15. Acari

The subclass Acari consists of two major groups of arachnids, the mites and the ticks, of which the first group will be discussed here, as ticks are less prevalent in the soil.

The suborder Oribatida (in the order Sarcoptiformes) comprises more than 10,000 species worldwide (Subías, 2004, 2013), excluding Astigmata, which has recently been recognised as a cohort of the Oribatida (Krantz and Walter, 2009; Norton, 1994). Most oribatids inhabit the soil-litter system, with a few arboreal and aquatic taxa (Schatz and Behan-Pelletier, 2008). Adults have a strongly sclerotised exoskeleton and are small (mainly 300–700 μm, with extremes from 150 to 2000 μm). Oribatid mites are often the dominant group in organic soils. In temperate forests densities may exceed 100,000 individuals comprising 100–150 species per m^2 (Norton and Behan-Pelletier, 2009). More than 430 species are known for South Africa (Fig. 7).

Oribatid mites play an important role in the decomposition of plant material (Schneider et al., 2004). The vast majority are either generalist particle-feeding saprophages, primary decomposers for breakdown of plant debris, or mycophages, secondary decomposers who, through feeding on fungi, release nutrients trapped in vegetation back into the soil. Most mesostigmatic mites are predators, some of which play an important role in biological control. For example about 20 species in the family Phytoseiidae are are commercially reared to control phytophagous mites on agricultural crops (Gerson et al., 2003).

Members of the saprophytic Oribatida prefer soils rich in organic matter, while Trombidiformes are more abundant in soils low in organic matter, where they probably feed on Protozoa and Bacteria. However, this correlation does not imply that the

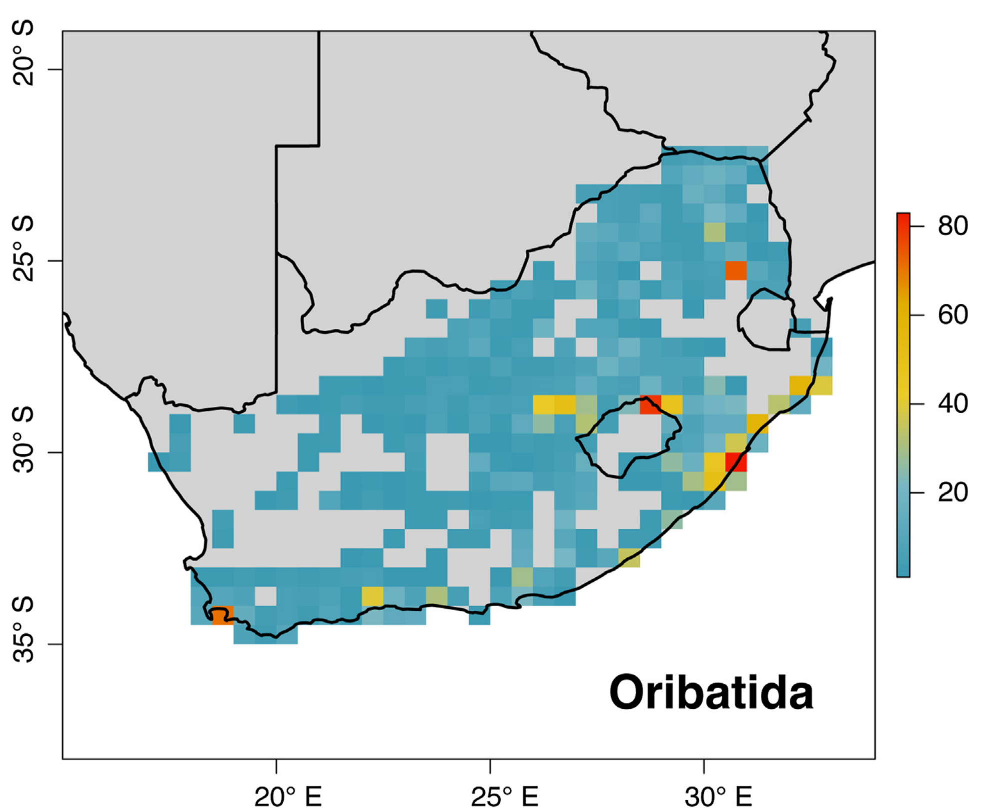

Fig. 7. Species richness distribution for oribatid mites in South Africa.

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Trombidiformes actually occur in higher numbers in biotopes with a relatively low percentage of soil organic matter than in those with a higher percentage. For example, a maximum density of 120,000 per m^2 Trombidiformes were found in rich subtropical forest soil, compared to a maximum of 38,000 per m^2 in pasture soil with a relatively low percentage of organic matter (Loots and Ryke, 1966a,b,c, 1967).

About 19 100 Mesostigmata species are known worldwide. The majority are free-living predators, inhabiting soil, litter, compost, manure, carrion, bird nests, house dust or fungi. Some species are arboreal or aquatic while others are parasites of mammals, birds, reptiles or arthropods. Mesostigmatic mites range in size from 200 to 4500 μm and are usually covered with well sclerotised dorsal and ventral shields (Lindquist et al., 2009). More than 281 species have been recorded in South African soils.

The heterogeneous group of trombidiform mites comprises of more than 22,000 species, which include a huge variety of terrestrial, aquatic and marine predators, phytophages, saprophages and parasites. These mites are mostly weakly or incompletely sclerotised and vary from 100 to 12,000 μm (Walter et al., 2009). More than 700 species are known from South Africa (Fig. 8).

3.15.1. Taxonomy and collections

The first studies of oribatid mites in South Africa were undertaken at the University of the Free State, Bloemfontein, by R. van Pletzen in 1959. From 1969 research continued at the National Museum, Bloemfontein. Since 1960, 61 taxonomic and 15 non-taxonomic papers on oribatids have been published of which 51 papers were by National Museum researchers. The National Museum is the only institution in South Africa (and in Africa) where taxonomic research on oribatid mites is carried out. Two acarologists are currently active at the Museum.

Lawrence undertook the first studies of Mesostigmata and Trombidiformes at the University of Cape Town and at the KwaZulu–Natal Museum from 1921. Zumpt contributed extensively to our knowledge of the parasitic mites of southern Africa as well as other African countries, while P.A.J. Ryke established Acarology at the Potchefstroom University resulting in the training of several mite specialists such as the well-known M.K.P. Smith Meyer. In addition, G. C. Loots, P.D. Theron, J. den Heyer, E.A. Ueckermann, P.A.S. Olivier and 33 students and researchers from North West University have worked on mites (Theron, 1982). Research by the aforementioned researchers and students resulted in close to 200 papers on the taxonomy of soil-dwelling mites, mostly from the southern African subcontinent, whereas another 40 dealt with ecological aspects of the soil mesofauna component. The Research Unit for Environmental Sciences and Management/Zoology, North–West University, Potchefstroom Campus and the Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI), Biosystematics—Arachnology are the only institutions in southern Africa where taxonomy on mesostigamatic and trombidiform mites is carried out, with three Acarologists involved.

The Oribatida collection of the National Museum currently consists of 4617 samples (i.e. collection localities) comprising more than 270,000 specimens. Holotypes of most species described from South Africa are deposited in the Museum's collection (260 holotypes).

All Mesostigmata and Trombidiformes type material are deposited in the collections of Zoology (North–West University, Potchefstroom Campus), Biosystematics (ARC-PPRI) and in the KwaZulu–Natal Museum. Zumpt's collection of parasitic mites was donated to the ARC-PPRI, Biosystematics, in 1983. The mite collection of the ARC-PPRI—Arachnology comprises 63,312 slide mounted mites, representing 2047 type species, 159 families and 690 genera.

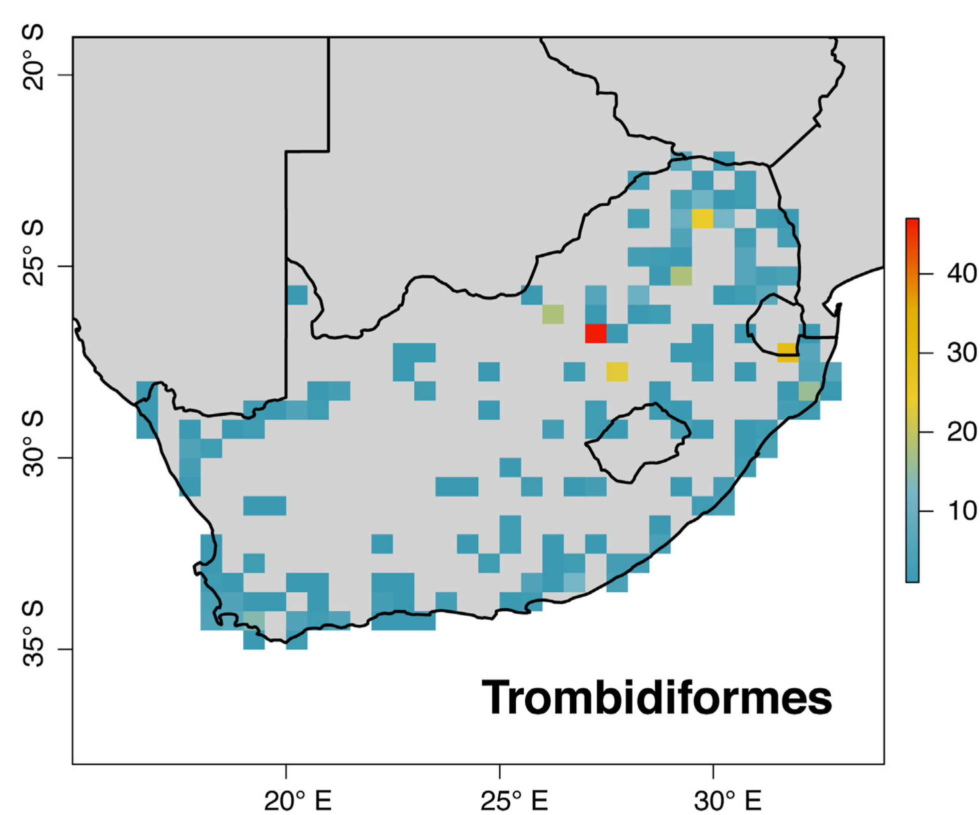

Fig. 8. Species richness distribution for trombidiformid mites in South Africa.

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3.15.2. Sampling

Mites are extracted by means of Tullgren funnels, beating and washing. The specimens are collected either directly into 70–75% ethanol as preservative, or dry: i.e. directly into a 10 mL Polytop vial without any preservation fluid. After 24 h the material is sorted under a stereomicroscope, using a fine brush. Oribatid mites are collected into micro centrifuge tubes with 70% alcohol to which 5% glycerol has been added to minimise brittleness.

3.15.3. Future research

The ecology of Oribatida in South Africa has been poorly studied. There has been no standardised sampling and arid regions have been poorly sampled. Many samples have been identified only to genus level. Identification keys are lacking; the most advanced key available (Family level) is that of Norton and Behan-Pelletier (2009). Although the genus level key of Balogh and Balogh (1992) is outdated, it is still suitable and often used. For South African species, there are only species level keys for selected genera. In addition, the large number of unknown oribatid mites hinders progress in other areas such as ecosystem services and their use as potential indicators.

Since 1959 surveys by the ARC-PPRI collected Mesostigmata and Trombidiformes in forest floors, savanna and *Acacia* biotopes, arid regions, citrus orchards, on natural vegetation and crops across South Africa, mainly for taxonomical studies. Most samples are identified to species level with more than 50 keys compiled for families and genera. After 1992 national surveys almost came to a standstill and was replaced by international collaborations. However, recently an attempt to turn the focus back to the study of local mites was made by a search for potential mite predators on Solanaceae and tea, both as part of international projects. Nevertheless, the decline in the number of Acarology taxonomists is of grave concern and may impact negatively on future research.

3.16. Microcoryphia (=Archaeognatha)

This order of bristletails was named Microcoryphia by Verhoeff on 22nd April 1904, and Archaeognatha by Börner eleven days later. Both names can be used as the International Code of Zoological Nomenclature does not apply to the names of orders. Microcoryphians, or hump-backed bristletails, have a shrimp-like appearance created by their long antennae, strongly arched tergites and continuity between the thorax and abdomen. They are up to 20 mm long. Although their mandibles are traditionally regarded as monocondylous, one of several features that would exclude them from being true insects, this interpretation has recently been challenged (Blanke et al., 2015). They live in humid microhabitats in decaying leaves and wood, and under bark and loose rocks, and one South African species was caught in a cave (Wygodzinsky, 1969).

There are two families, Meinertellidae and Machilidae, jointly containing 65 genera and 520 species. The Meinertellidae lack scales on the legs and antennal base. South Africa hosts four of the 18 genera, and 21 species (all endemic but one) (Wygodzinsky 1955, 1969). The Machilidae are boreal and might be paraphyletic; none of the 47 genera and 362 species are known from southern Africa (Sturm and Bach de Roca, 1993; Sturm and Machida, 2001).

Males deposit spermatophores or sperm droplets, and females lack a spermatheca, which implies that they collect spermatophores regularly. Adult females use their ovipositor to place clutches of eggs in crevices or soil once per moult. Nymphs resemble adults but hatch without body scales, and may reach maturity after about five to nine moults, which continue in adulthood. Development can take months to years, and specimens have lived four years. Generally agile and nocturnal, bristletails scavenge plants, lichens and arthropods. Bristletails can jump several centimetres by suddenly flexing their abdomens. There have been no physiological or ecological studies of southern African species (cf. Lawrence, 1953a).

3.16.1. Taxonomy and collections

Biogeographically, the Meinertellidae are predominantly austral, and the Machilidae are mostly boreal. The southern African fauna is dominated by Machiloides, which also occurs in East Africa, Madagascar, Chile, Argentina, Tasmania, Spain and Virginia (USA). The genus *Machilinus* is found in the Western Cape, Europe, North America and Argentina, the only African genus being allied with the European fauna. The presence of the genera *Machilellus* and *Hypomachilodes* in southern Africa is debateable (Wygodzinsky, 1955). Individual species are insufficiently sampled to draw many biogeographical generalisations, but there appears to be distinct groups of species in the Western Cape and KwaZulu–Natal.

Wygodzinsky (1955, 1969) described the bulk of the species from material lodged in the Lund Museum (Sweden), but there are specimens in the KwaZulu–Natal Museum (South Africa), the Naturhistoriska Riksmuseum (Sweden) and the American Museum of Natural History (New York, U.S.A.).

3.16.2. Sampling and identification

Grassland and forest bristletails can be caught in pitfall traps and forest species can be extracted from leaf litter using Tullgren funnels (see e.g. Dindal, 1990; Martin, 1977; Schauff, 2001 for descriptions of methods). Hand collecting from leaf litter and tree trunks or turning of logs and stones may also be productive. Species can be identified using the taxonomic keys provided by Wygodzinsky (1955, 1969).

3.16.3. Future research

Work has recently been started on barcoding the South African species as a step towards establishing their biogeographical distributions, habitat associations and population densities.

3.17. Diplura

Diplurans, or two-pronged bristletails, are pale, wingless, eyeless invertebrates with moniliform antennae, elongated abdomens and obvious cerci. Diplurans occur under rotting leaf litter, logs, bark, stones and similar damp microhabitats, especially in forests. There are about 924 extant species in 125 genera worldwide, classified into six to ten families.

Species in the family Campodeidae generally eat fungi, mites and springtails, while parajapygids and japygids prey on springtails, myriapods, isopods, insect larvae and other diplurans. There have been no physiological or ecological studies of southern African species (cf. Lawrence, 1953a).

3.17.1.1. Taxonomy and collections

The first southern African species was described by Meinert (1865) and the second by Peringuey (1901). Monographic works then followed from Silvestri (1913, 1931, 1932, 1948), Condé (1950, 1955a, 1956) and Pagés (1952, 1955), partly fuelled by the collecting of R.F. Lawrence, B. Hanström, P. Brinck and G. Rudebeck (Condé, 1950, 1955a,b; Pagés, 1955). The South African species are listed online (Villet, 2000–2015). The families Campodeidae, Projapygidae and Japygidae occur in southern Africa: Campodeidae includes 27 species from seven genera; Projapygidae comprises two species from one genus; and Japygidae contains 10 species from three genera. Based on recent sampling, their true diversity is likely higher than this (L. Deharveng and A. Bedos, pers. comm.).

Biogeographically, some species e.g. *Campodea fragilis*, are cosmopolitan and may be introduced, while *Campodea barnardi* also occurs on the Canary Isles and may have originated from South

Africa. The genera *Campodella* and *Silvestricampa* are endemic to South Africa, and *Natalocampa* occurs only in Chile and South Africa (Allen, 2002); other genera are more widespread, but limited sampling in many countries needs to be addressed before endemicity can be determined.

Silvestri's dipluran collection is in the Museo Civico di Storia Naturale di Genova, Italy, and there is a collection of South African Diplura in the Lund Museum, Sweden.

3.17.2. Sampling and identification

Diplurans, especially campodeioids, are easily extracted from samples of leaf litter with Tullgren funnels or Winkler bags (see e.g. Dindal, 1990; Martin, 1977; Schauff, 2001 for descriptions of methods). The large-bodied japygoids can be hand-collected from leaf litter or by turning of logs and stones in suitable habitats. Species can be identified using the taxonomic keys published by Condé (1955a) and Pagés (1955).

3.17.3. Future research

A barcoding study of the South African species has been initiated, and will be followed by research on their biogeographical distributions, habitat associations and population densities.

3.18. Protura

Proturans are pale, distinctly elongated, small (<2 mm long), prognathous invertebrates that lack eyes, wings, cerci and a hypopharynx; pseudoculi apparently replace their antennae. They feed on ectomycorrhizal fungi and can be found in humid soil samples containing roots or moss.

There have been few physiological or ecological studies of any proturan species (cf. Lawrence 1953a). They can be abundant (Krauß and Funke, 1999) in humid habitats such as soil, litter, moss and caves, and feed on mycorrhizal fungi and decaying plant matter (Machida and Takahashi, 2004; Malmström and Malmström, 2011).

3.18.1. Taxonomy and collections

There are over 788 species in 72 genera globally (Tuxen, 1964; Szeptycki, 2007; Pass and Szucsich, 2011). The order includes three superfamilies, Eosentomoidea, Acerentomoidea and Sinentomoidea; only the latter is not known from South Africa. Eosentomoidea contains one family with three subfamilies and nine genera. Szeptycki (2007) recognises three families in the Acerentomoidea.

The families Eosentomoidae and Acerentomoidae occur in southern Africa (Condé, 1955b), but in South Africa, only an unidentified species of *Eosentomon* from the Tsitsikamma area has been recorded (Condé 1955b), and two species of Acerentomidae (Berlese, 1908; Womersley, 1931), both of which have been found on at least two other continents (Tuxen, 1964; Szeptycki, 2007), and were probably introduced. Unidentified proturans have recently been recovered from Hogsback (M.H. Villet, pers. obs.).

While good progress has been made in proturan taxonomy globally (Tuxen, 1964; Szeptycki, 2007; Pass and Szucsich, 2011), there are few studies on their biology or ecology anywhere in the world, and no physiological or ecological studies of southern African species (cf. Lawrence 1953a).

3.18.2. Sampling and identification

Proturans can be recovered from humid soil samples containing roots or moss with Tullgren funnels or Winkler bags. The two species known from South Africa can be identified by referring to Condé (1955b).

3.18.3. Future research

Proturans are essentially unstudied in southern Africa, so research could go in any direction. Recent fieldwork has located proturans in the Eastern Cape; these are being barcoded and further field surveys are under way.

3.19. Collembola

Collembola (springtails) are small (2–4 mm) primitive wingless invertebrates (Apterygotes) and amongst the most abundant and widespread organisms in the world, being especially common in soil (Hopkin, 1997). They are believed to be more closely related to crustaceans than insects (Nardi et al., 2003). They are best recognised by their unique forked jumping organ, or furca, folded under the abdomen, and a ventral tube, an abdominal organ used for water balance.

3.19.1. Taxonomy and collections

To date there are an estimated 30 publications on Collembola recorded or described from South Africa; the earliest from Börner (1908). Lawrence (1953a) drew attention to the diversity and functional importance of litter and soil biota in South Africa. Most notably, comprehensive descriptions were made by Paclt (1959, 1964, 1965, 1967), Coates (1968a, 1968b, 1969, 1970) and later Barra (1994, 1995, 1997, 1999, 2001, 2002); Barra and Weiner (2009). Since 2008 bilateral South Africa–France Protea I and Protea II project has sampled the Cape Floristic Region extensively with the aim to investigate the taxonomic and genetic diversity of Collembola in the Fynbos Biome (Janion et al., 2011).

There are currently about 8 200 species of Collembola known worldwide (Bellinger et al., 1996–2016) and they play an important role in decomposition, litter fragmentation and soil formation (Rusek, 1998). From the literature, 124 species from 61 genera and 17 families have been recorded from South Africa. Of these, a total of 25 species are thought to be introduced, 75 endemic, and 24 are widespread (Janion-Scheepers et al., 2015). The majority of species were recorded from the Western Cape (77 species), KwaZulu–Natal (49 species) or the Eastern Cape (20 species), while records from the other provinces range from one to eight species (Fig. 9). There are currently six genera endemic to South Africa: *Najtafrica* (Neanuridae), *Probrachystomellides* (Brachystomellidae), *Capbrya* (Entomobryidae), *Lepidokrugeria* (Entomobryidae), *Neophorella* (Tomoceridae) and *Tritosminthurus* (Bourletiellidae). *Neophorella dubia* was described from a single specimen and is the only endemic species of the family Tomoceridae to occur in South Africa. However, after intensive sampling in the Cape Town region (the exact type locality of this specimen is not known), no example of this species has been found, suggesting that this may have been a misidentification.

3.19.2. Sampling and identification

Various sampling techniques have been used to collect springtails from as many localities and different microhabitats as possible, including Afromontane forest, different fynbos vegetation types, intertidal habitats, caves and disturbed areas such as gardens and agricultural areas. Leaf litter, moss, rotten wood and soil samples (500 mL or 1 L) are taken at different sampling sites, and occasionally sieving and pitfall traps are also used. Only two ecological studies on Collembola have been published (Liu et al., 2012; Leinaas et al., 2015). The first study also showed that about 10 samples are sufficient to capture most of the species richness in an ecologically homogeneous area in the Western Cape (Liu et al., 2012). Litter samples are extracted by means of a Tullgren funnel for five to seven days, or until dry (Berlese, 1905; Tullgren, 1918). In addition, active searching is done in the field; soil is washed next to rivers to collect water-dependent species, which are collected with a fine brush. Fine sand is washed in the laboratory and animals collected with a brush. Vegetation such as branches from bushes, fynbos shrubs, and grass is beaten

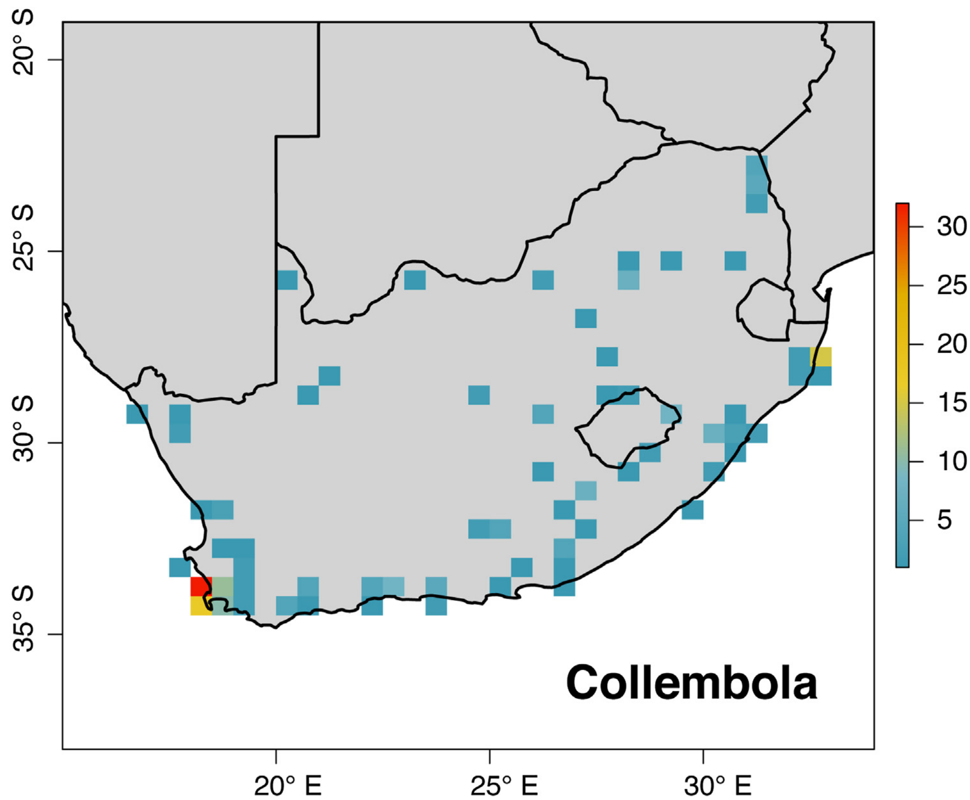

Fig. 9. Species richness distribution for springtails in South Africa.

over a tray and animals are collected by means of an aspirator. Finally, litterbags can be used to investigate decomposition rates, with Collembola being extracted by means of a high-gradient extractor (for details see Bengtsson et al., 2011, 2012; Leinaas et al., 2015).

The current available taxonomic expertise in South Africa was established through a bilateral project (Janion et al., 2011). Several projects on springtail physiology and systematics of Collembola are underway at Stellenbosch University, and further groups around the country are starting to include them in their research. The majority of the T.J. Coates collection is deposited at the ARC-PPRI, while several holotypes are deposited at the Iziko South African Museum. Other holotypes are assumed to be at museums abroad, but are rarely mentioned in earlier descriptions. Available European keys are used (Fjellberg, 1998, 2007; Potapov, 2001) but for local species only species descriptions are available. Another source of information, links and an up-to-date list is the website *Collembola of South Africa* (http://collembola.co.za/).

3.19.3. Invasive species

About 20% of Collembola species are thought to be introduced to South Africa, mostly found in disturbed environments, in gardens or close to human settlements (Janion-Scheepers et al., 2015). These species are usually of European origin, which is not surprising given the close historical links between South Africa and Europe (Giliomee and Mbenga, 2010). The most well-known collembolan pest species include the Lucerne flea *Sminthurinus viridis*, which is thought to have been introduced from Australia (Wallace and Walters, 1974).

3.19.4. Future studies

Many large areas and biomes, such as the forest and savannah remain undersampled, thus many species likely remain to be discovered. To understand the diversity of Collembola, the combined use of traditional taxonomy and modern molecular barcoding techniques may help to compensate for the current lack of taxonomic skills and facilitate the exploration of complex specific clusters. Rapid progresses in the taxonomic knowledge of South African Collembola through knowledge transfer projects (Janion et al., 2011) are expected to contribute to the understanding of their role in ecosystem functioning and their response to habitat transformation. However, there is a need to collate information and develop keys for South African species. As they do represent a large proportion of the total assemblage in soil, this group could be used to assess the effect of environmental changes and habitat disturbance, as has been done elsewhere (Deharveng, 1996; Cassagne et al., 2006).

3.20. Insecta

The considerable species richness of insects (conservative estimated richness of 87,000 species in southern Africa; Scholtz and Chown, 1995), their huge biomass (e.g. >four times that of vertebrate biomass in tropical systems; Fittkau et al., 1973), and their involvement in all trophic levels (e.g. as predators, prey, parasites, and detritivores; Grimaldi and Engel, 2005) makes them integral to both above- and below-ground ecosystems. Insects make up a significant part of soil communities; a review of the ~30 insect orders indicate that virtually all of them, from Thysanurans to Hymenoptera, are represented in the soil to some degree (McColloch and Hayes, 1922). This representation can range from species spending a temporary and inactive component of their life-cycle in the soil (e.g. lepidopteran pupae), to a temporary but active component of their life-cycle (e.g. neuropteran larvae), and even highly specialised soil-adapted species that are soil dependant/obligates (e.g. termites) (Menta, 2012). The relative

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importance of these broad groups towards soil ecology ranges from less important for those temporary, inactive species towards high ecological importance of the latter two groups, which play essential roles in the chemical, physical and biological processes operating in the soil (Anderson, 1988). For example, many soil insect species are associated with the fragmentation and decomposition of dead organic material and nutrient recycling, while the larger-sized macrofaunal insect components impact on the physical structure of soils through their shifting of large quantities of soil through burrowing and feeding activities, with two groups recognised as soil ecosystem engineers (see termite and ant sections below). Overall, soil-associated insects also have strong influences on above-ground processes through feedbacks, such as on plant diversity and community structure (De Deyn et al., 2003; Wardle et al., 2004; Johnson et al., 2008), and many insects whose larvae live in the soil, play key ecosystem roles above ground as adults, such as pollination (e.g. Gess and Gess, 2004b).

There are specific sections dedicated to Formicidae, Termitoidae (termites), and Scarabaeinae below, here we briefly review other insect groups that are important components of the soil fauna. Estimates of southern African species numbers are given for the southern Africa region, as defined by Scholtz and Holm (1986), except where such information is known specifically for South Africa. More information on the collection, preservation and collections can be found in references given in each group, and is not discussed in detail here.

Order Blattodea (Cockroaches, worldwide 4641 species, Inward et al., 2007; Beccaloni and Eggleton, 2013; and termites, 2929 worldwide, Krishna et al., 2013) contains many of the roughly 230 cockroach species (six families; 20 endemic genera) in southern Africa that are associated with soil habitats, either superficially as a medium in which to deposit their egg cases (ootheca), or as their primary habitat, e.g. *Blepharodea discoidales* (Blaberidae) found burrowing in the upper surface layers of organically rich soils in the winter-rainfall Cape. Many southern African members of the speciose families Blaberidae and Blatellidae are apterous and appear to be adapted for burrowing in soil and leaf litter. The winter-rainfall regions of the Cape have a large endemic component of species of Blaberidae, including burrowing species in the genera *Aptera* and *Blepharodea*. Termites (Termitoidae, formally Isoptera) are discussed in more detail below.

Order Embiidina (Embioptera, webspinners; worldwide about 360 species; Miller et al., 2012)—species of this unusual order live within silken tubes (galleries), which they spin under rocks, bark, between leaves, or in the soil. Approximately 37 species (11 genera) are known from southern Africa. Species of Embiidae are known to utilise soil habitats, particularly in seasonally dry areas where they feed as detritivores on dead vegetation.

Order Orthoptera (Grasshoppers, katydids, and crickets; worldwide ca. 25,000 species)—a rich diversity of orthopterans is found in southern Africa (ca. 765 species; 338 genera; 18 Families), with large numbers of regional endemic species in the western, arid parts of South Africa, e.g. within the families Pneumoridae and Lentulidae. Orthopterans occupy a diverse array of terrestrial habitats with many species showing linkages and adaptations towards leaf-litter and soil habitats. Most orthopteran species are in the sub-order Ensifera (crickets and katydids). These species show a range of adaptations towards fossorial activities, such as the loss of wings and modified fore and hind legs for digging. The best known of these include the mole crickets (Gryllotalpidae; one southern African genus *Gryllotalpa*, three species, one South African endemic), the burrowing crickets (Gryllidae; 70 South African species), and the dune crickets (Schizodactylidae; seven South African species). Charismatic species of Gryllidae include the largest cricket in the world found in the northern parts of South Africa, *Brachytrupes membranaceus*. Amongst the dune crickets, the genus *Comicus*, endemic to the sandy areas of south-western southern Africa, shows remarkable enlarged projections to their hind tarsi for digging through, and locomotion on, soft sand. Many species of short-horned grasshoppers (sub-order Caelifera) deposit their eggs in the upper soil layers (e.g. Acrididae, 356 South African species), including the plague species of brown locust *Locusta paradalina*, which forms periodic outbreaks of swarms in the Karoo region. Other geophilous orthopterans show specific adaptations, as seen in species of Pamphagidae that mimic the soil and pebble colours (e.g. toad grasshoppers of the genus *Trachypetrella* on the arid quartz pebble plains). Tetrigidae species frequent soils close to water to escape predators by jumping into the water and to feed on the damp soils, absorbing organic particles. The greatest adaptations towards living in the soil is found in the short-horned grasshoppers, the Tridactyloidae (pygmy mole-crickets). Their fore and hind legs are adapted to fossorial digging activities, allowing them to feed on a damp soil diet, including algae and bacteria.

Order Psocoptera (Booklice; worldwide ca. 5550 species; Aldrete, 2006)—although individuals of this order are tiny (1–10 mm), they can occur in leaf litter and soil in huge numbers, where they play an essential role in breaking down organic matter (Persson et al., 1980). Southern Africa has about 80 species in 34 genera, although this is most likely a large underestimate.

Order Hemiptera (Bugs, aphids and cicadas; worldwide > 80 000 species)—a hugely diverse order of insects, with most species associated with different parts of plants (Schuh and Slater, 1995). However, several different families and sub-families across the three sub-orders in southern Africa, have species that are closely linked to soil habitats. The tiny predacious gnat bugs (Enicocephalidae; 40 species and eight genera from southern Africa) are found in leaf litter and loose soil. The phylogenetically important Thaumastellidae, with two of only three known world species endemic to the succulent Karoo (*Thaumastella namaquensis* and *T. elizabethae*) are found in small chambers in the soil (Schuh and Slater, 1995). Some predatory assassin bugs (e.g. Stenopodinae and Reduviinae) are closely linked to the soil, with nymphs often covering their bodies with sand and soil particles as camouflage, and adults laying their eggs in the ground. Some true bugs actively burrow in the soil, such as the burrowing bugs of the family Cydnidae (30 species and ten genera from southern Africa), which can reach depths of two metres, where they feed on roots of plants. Other hemipterans of the sub-order Auchenorrhyncha that have specialised on root feeding include the Tettigometridae (two species from southern Africa), Cixidae (24 species from southern Africa), Cercopidae (33 species from southern Africa), and the Cicadidae (140 species from southern Africa). Amongst the third hemipteran sub-order Sternorrhyncha, sap-feeding aphids (Aphididae) and scale-insects are commonly found feeding below ground on the roots and other parts of plants. Several species found in the latter two sub-orders (Auchenorrhyncha and Sternorrhyncha) have close and interesting mutualistic associations with subterranean ant species. Many species within the root sap feeding groups are considered serious agricultural pests in South Africa (Prinsloo and Uys, 2015).

Order Neuroptera (Lacewings, worldwide species 142, Sole et al., 2013, and antlions, worldwide species ca. 2000, Mansell 1999)—twelve of the world's 17 families of lacewings are represented in southern Africa and the south-western and central arid region of South Africa is considered a global centre of endemism and adaptive radiation for the two soil associated families Nemopteridae (72 species, 14 genera in southern Africa; 38% of the world's fauna endemic to the region; Sole et al., 2013) and Myrmeleontidae (180 species, 50 genera in southern Africa; Mansell, 1996; Mansell and Erasmus, 2002). The larvae are mostly soil living and are considered to be specialised and keystone predators. The biology of individual species of Nemopteridae is poorly known, but most species appear to live freely in the sand, although some Crocinae live in soft sands under rock overhangs and cave entrances. Antlion larvae also complete their life-cycle in the soil, with larvae free living in the soil ambushing invertebrate prey, or with some species across three genera constructing a small tunnel-shaped pit to trap prey.

Order Coleoptera (Beetles; worldwide species > 350,000 species)—the world's most speciose insect order is well-represented in southern Africa (ca. 20,000 species) with several sub-families and tribes showing centres of diversity and adaptive radiations in the region (Colville et al., 2014). At least 35 different families of beetle, incorporating several thousand southern African species, utilise the soil as a primary habitat for their larvae and/or adults. Soil beetles serve key functions as detritivores (e.g. Cetoniinae, Dynastinae, Melolonthinae, Elateridae), predators (e.g. Carabidae, Cicindelidae, Staphylinidae, Trogidae), and herbivorous root feeders (e.g. Buprestidae, Tenebrionidae, Chrysomelidae). Some notable examples of beetle groups showing centres of diversity and endemism in South Africa that are intimately linked to soil habitats, include the tribe Hopliini (ca. 1200 southern African species, making up ca. 65% of the world's species), subfamily Cetoniinae (250 southern African genera, making up ca. 50% of the world's genera), subfamily Scarabaeinae (making up ca. 27% of the world's genera, see below), and the arid adapted Tentyriinae darkling beetles (ca. 1200 southern African species, making up ca. > 60% of Afrotropical species) in the family Tenebrionidae.

Order Diptera (Flies; worldwide species ca. 150,000 species; Wiegmann and Yeates, 2007)—one of the largest insect orders. Flies have important ecologically roles in soil habitats as well as significant medical and economic impacts. Fly larvae play an essential role as detritivores and predators in soil habitats, where larval abundance and biomass can reach impressive values (Menta, 2012). Amongst the ca. 6500 southern African species, major families to be found in South African soil habitats include Tipulidae (250 species in the region), Bibionidae (18 species in the region), Startiomyidae (112 species in the region), Tabanidae (230 species in the region), Rhagionidae and Vermelionidae (28 species in the region), Mydidae (195 species in the region), Asilidae (ca. 500 species in the region), and Empididae (220 species in the region). Adults of Mydidae, Tabanidae, Vermelionidae, and Empididae show high species richness and endemism and pollinating co-evolutionary relationships with the flora of the fynbos and succulent Karoo (see Colville et al., 2014).

Order Lepidoptera (butterflies and moths; worldwide species ca. 160,000 species; Kristensen et al., 2007) – the larvae of a significant number of southern Africa's ca. 6800 moth and butterfly species utilise the soil solely as a protective medium in which to pupate. Larvae typically feed on plants, then migrate to the ground, burrow into the soil where they continue their life-cycle. Only a relatively small number of South Africa's lepidopteran species utilise the soil as the primary habitat for their larval stage. Amongst the moths, the members of the ghost moth family Hepialidae (ca. 80 species in southern Africa) live exclusively underground, tunnelling in the soil and feeding on roots (Grehan, 1989). Similarly, species of owlet moths in the sub-family Noctuinae (ca. 100 species in southern Africa) live in the soil feeding on roots of seedlings, although some species will come up to the surface from burrows to feed on leaves. The latter two moth groups are of considerable economic importance in South Africa as garden and crops pests, e.g. the notorious cutworm (*Agrotis segetum*, Noctuidae; see Prinsloo and Uys, 2015). Amongst South Africa's butterflies, only species of the family Lycaenidae show below ground habitat usage, either through their association with certain ant species and their underground nests, or through their feeding on the rootstocks of specific host plant species. The larval stages of certain species within the genera *Aloeides*, *Chrysoritis*, *Lepidochrysops*, *Thestor*and *Trimenia* have evolved ant associations, most notably with *Anoplolepis* and *Camponotus* ant species (see ants section below). The larvae of the genus *Orachrysops* all appear to be rootstock feeders on species of *Indigofera* (Fabacaeae) (Terblanche and Edge, 2007; Edge and Van Hamburg, 2009). Larvae spend all their time underground from the third instar on, and pupate alongside the rootstock of their host plant. Both the larvae and the pupae are tended by *Camponotus* ant species. The family Lycaenidae contains many South African endemic species, with a particularly high concentration of narrowly distributed species of high conservation importance in south-western Cape fynbos habitats (Mecenero et al., 2013).

Order Hymenoptera (bees and wasps; worldwide species ca. 115,000 species, Formicidae discussed below)—at least 20 different wasp and bee families found in South Africa utilise the soil to some degree, either through excavating tunnels, burrows, or cavities, or using existing nests or cavities; or through the use of soil as a building material for their nests, which are often situated away from the soil habitat (see Gess and Gess, 2014). In these nests and burrows, wasps and bees rear their young, providing them with provisions of, for example, pollen or invertebrate prey. The fundamental ecological importance of wasps and bees as parasites, predators, and pollinators makes them one of the most important soil associated insect groups in South Africa. They are of also considerable conservation importance, with South Africa housing a significant number of the world's bee species (1140 species); ca. 5% of global bee species, including some of the earliest diversifying lineages, and high numbers of local endemics (Kuhlmann, 2009). Similarly, amongst the wasps (>4000 South African species; Simon Van Noort pers. comm.), high diversity and endemism are seen in groups with soil associations, e.g. 141 of the world's 350 masarine wasp species (Vespidae: Masarinae) are restricted to southern Africa (Gess and Gess, 2004a). The Formicidae are discussed below.

3.20.1. Termitoidae

Termites are eusocial insects which, until recently, were classified within the Order Isoptera. Recent DNA evidence in support of the hypothesis, originally based on morphology, that termites are highly modified roaches, has led to the acceptance of the monogeneric family of wood roaches, Cryptocercidae (*Cryptocercus*), as the definitive sister group to the termites. This necessitated the demotion of the termites to a subordinate taxon to reflect their phylogeny. Consensus on the accepted classification is yet to be achieved (Inward et al., 2007; Beccaloni and Eggleton, 2013; Krishna et al., 2013), although the classification of the termites as an epifamily (i.e. Termitoidae) is widely used in the literature.

Relative to most insect groups, termites have low species diversity, although the southern African region has an unusually genus-rich fauna for an area so far south. Currently 39 genera and 126 described species, a third of which are endemic, are known from South Africa. These numbers will certainly increase with further study of the southern African fauna.

3.20.1.1. Taxonomy and collections. The foundation of termitological studies in South Africa was laid by C.W. Fuller, who established the National Collection of Isoptera and published widely on the local fauna (e.g. Fuller, 1915, 1922, 1925a,b, 1927). Succeeding Fuller, W.G.H. Coaton, in addition to publishing extensively on the control and biology of termites, initiated a national survey of Isoptera and over a period of almost 20 years systematically surveyed the distribution of termites in South Africa, Namibia, Zimbabwe and Swaziland, amassing a comprehensive collection of more than 35,000 colony samples.

This survey remains the most complete faunistic survey ever undertaken on any group of animals anywhere in the world, and resulted in numerous publications (Coaton and Sheasby, 1973a, 1973b, 1973c, 1973d, 1974a, 1974b, 1974c, 1975a, 1975b, 1976a, 1976b, 1977, 1978a, 1978b, 1979, 1980). This information has since been collated by Uys (2002). Others who have contributed to our knowledge of the South African termite fauna include J.E. Ruelle, R. M.C. Williams, W.A. Sands and V.M. Uys through the publication of various works on the Afrotropical fauna (e.g. Sands, 1957, 1959, 1965, 1969, 1972, 1992, 1995, 1998, 1999; Williams, 1966; Ruelle, 1970, 1975, 1978, 1979, 1992; Uys, 1994a,b, 2002).

Several seminal works on termites have been published over the last four decades and include two comprehensive volumes: *Biology of Termites* by Krishna and Weesner (1969, 1970) and *Termitologia* in three volumes, published by Grasse (1982, 1984, 1985), both these works remain invaluable references; Abe et al. (2000) *Termites: Evolution, Sociality, Symbioses, Ecology* and more recently, *Biology of Termites: A Modern Synthesis* edited by Bignell et al. (2010). The most recent and comprehensive compilation is the monumental seven volume *Treatise on the Isoptera of the World*, by Krishna et al. (2013).

The extensive termite collection referred to above, in addition to a large nest collection and reprint library, are housed at the Biosystematics Division of the ARC-Plant Protection Research Institute in Pretoria, with one taxonomist (V.M. Uys) responsible for research and curation.

3.20.1.2. Sampling and identification. The subterranean habits and often sporadic activity of termites makes sampling them less straightforward than other insect groups. Active searching transects are an effective sampling method in wetter habitats, particularly rainforests (Jones and Eggleton, 2000), but are less effective in drier regions. In southern Africa, baiting with cellulose baits has been used effectively (Schuurman, 2005; Davies et al., 2013), but this only samples wood-feeding termites. A combination of these methods is therefore often used in such environments (e.g. Davies et al., 2012). For mound-building termites, mound counts can be also be made, either through manual searching (Meyer et al., 1999) or remote sensing techniques (Davies et al., 2014). Useful comparisons of methods have been made by Zeidler et al. (2004) and Davies et al. (2013).

Termite genera and species often coexist and one should be mindful of this when sampling. The identification of termites is usually done using the soldier caste, as soldiers are distinctive and comparatively easy to identify. Keys to the termite genera of southern Africa, based on the soldier caste, are provided by Uys (2002). Workers, although always present and numerous, are cryptic and have been neglected by taxonomists in the past and are generally poorly described, if at all. Despite recent progress in the description and study of the worker caste, mostly due to the pioneering work of W. Sands, identification of workers remains complex. A key to genera based on the worker caste is provided by Sands (1998). Species level identification should be done by a specialist as access to a range of literature and reference material is required.

3.20.1.3. Invasive species. Introduced species have generally failed to thrive in South Africa. This is mainly due to efficient interception and subsequent eradication or unfavourable environmental conditions, including competition for food supplies by indigenous species, adverse climatic conditions inland and predation by the introduced Argentine ant (Coaton and Sheasby, 1976a, 1979). For a worldwide review of invasive termites see Evans et al. (2013).

3.20.1.4. Future research. Like all insect groups, much work still needs to be done on the systematics and ecology of termites. The main termite collection contains thousands of unidentified samples, mainly of genera in need of revision, including several key genera such as *Odontotermes*, *Microcerotermes*, *Microtermes* and *Cubitermes*. Revising these genera should be the focus of future taxonomic research. However, the sheer volume of material and the unsuitability of most of these samples for molecular work due to their age are significant factors hampering progress. Large gaps in our knowledge of the natural history of termites also exist. For example, little is known about the longevity of individual termite mounds and the dynamics of how mound distributions change over time. Such information would be useful in understanding their role in shaping heterogeneity over longer periods of time. In addition, quantifying the contribution of termites to a range of ecosystem services and how better to utilise them for increased agricultural production (Sileshi et al., 2009; Evans et al., 2011) should be investigated.

3.20.2. Scarabaeinae

In addition to fossorial dung-burial habits, scarabaeine dung beetle species show both free-flying and ground surface activity, which they use to move between and exploit mammalian droppings. Therefore, their functional ecology is dominated by responses to both edaphic and surface environmental factors (e.g. Doube, 1991; Davis, 1994, 1996a,b). Edaphic factors include (i) differences in ease of tunnelling due to variation in soil hardness with soil grain-size profiles (Hanski and Cambefort, 1991), and (ii) differences in rates of drainage and moisture retention, which may influence survivorship of immature stages (Fincher, 1973). Surface environmental factors include (i) responses to different microclimatic variables (temperature, light intensity) (Davis et al., 2013) and (ii) responses to different dung types (Davis, 1994).

Dung beetles occur throughout South Africa although species richness is greater in the warmer northeast climates (Davis, 2002) (sampling over one year in savannah, near Pretoria: 121 species, Hluhluwe Game Reserve: 113 species) where seasonal summer peaks in rainfall and temperatures co-occur. Species richness is least in the cooler southwest climates (sampling over one year in Mediterranean-type shrublands, Cape Peninsula: minimum 12 species, West Coast: maximum 33 species) where opposing seasonal peaks in winter rainfall and summer temperatures result in peak seasonal dung beetle richness during the mild moist spring and, to a lesser extent, the similar conditions in autumn. Thus, dung beetle colonisation and burial activity occurs primarily during periods in which rainfall events and suitable temperatures coincide (Davis, 1995, 1996c). Periods of unfavourably low temperatures and seasonal or unseasonal drought are mostly characterised by quiescence at the ends of tunnels in the soil as adults or as larvae within modelled masses of dung, termed broods.

3.20.2.1. Taxonomy and collections. Although 491 scarabaeine dung beetle species and 70 genera are currently listed for South Africa (Davis, 2013), the alpha taxonomy is incomplete as there are both undescribed species and taxonomic errors (A.L.V. Davis pers. obs.). In Gauteng Province, the National Collection of Insects (NCI), University of Pretoria (UP), and the Ditsong National Museum of Natural History (DNMNH) have major holdings of dung beetles as a result of the influence of the Australian CSIRO dung beetle introduction project 1965–1986 and the presence of curatorial staff with an interest in dung beetles. Type material is also held by the Iziko South African Museum owing to the interest shown in dung beetles by a past curator (L. Péringuey).

Past analysis of available data showed a group of widespread generalists plus climatic specialists centred on six principal biogeographical regions, winter and bimodal spring/autumn rainfall in the southwest, arid late summer rainfall in the southwest interior, southwest Kalahari deep sands, highveld

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grassland in the east, northeast savannah, and the subtropical east coast (Davis, 1997, 2002). Some species showed even more specialist distribution related to local ecological conditions within particular regions.

3.20.2.2. Sampling and identification. Although dung beetles have been harvested from droppings and the underlying soil (Paetel, 2002), pitfall trapping with dung baits is the most frequently used sampling method in South Africa as it lends itself to relatively easy collection of quantitative data (Spector, 2006) for all four behavioural types: (i) dung removal from droppings by ball rolling (telecoprids), (ii) dung removal to tunnels under a dropping (paracoprids), (iii) sequestration of dung buried by other species (kleptocoprids), or (iv) activity largely restricted to droppings (endocoprids). Sampling for dung beetles has been unevenly applied across South Africa according to available funding and areas of particular interest to researchers. Although some past studies were conducted over an entire year (Bernon, 1981; Davis, 1996a,b,c), most modern studies are short-term, localised, spatial studies.

Although many behavioural, ecological, biogeographical and systematics publications have resulted from research at the CSIRO Dung Beetle Research Unit, University of Pretoria Scarab Research Unit, and University of the Witwatersrand, there are no specific keys for South African dung beetles. However, identifications of genera (Davis et al., 2008) and some species found in South Africa (e.g. Zur Strassen, 1967; Ferreira, 1978; Scholtz and Howden, 1987; Barbero et al., 2003; Harrison et al., 2003) may be drawn from works on the Afrotropical fauna at large.

3.20.2.3. Future research. As land exploitation and the use of pesticides have become more widespread (Davis et al., 2004), dung beetles are ever more frequently used as biological indicators in conservation, land usage research, and ecological impact assessments (e.g. Botes et al., 2006b; Simelane, 2009; Jacobs et al., 2010; Davis et al., 2012). To assist interpretation of South African studies, more precise biogeographical and ecological data are required on each species. The current data-basing of dung beetles from three Gauteng museums (NCI, DNMNH, UP) will generate an improved distributional database for defining biogeographical regions. However, further data are required from these different regions to improve the functional ecological database. This necessity may be illustrated by findings from the Western Cape (Davis, 1993) where many endemic species from the winter rainfall region are found in natural shrubland whereas species from the summer rainfall region are found primarily in pastures resulting from clearance of natural shrubland. These results imply both changes in biogeographical distribution pattern and local patterns of habitat association with exploitation of the environment. In addition, there is limited knowledge of interactions between dung beetles and other members of the soil biota.

3.20.3. Formicidae

While some ant species are strictly subterranean, many soil-nesting ants do have substantial above-ground foraging activity and some ant species are strictly arboreal (Hölldobler and Wilson, 1990). Soil nesting ants act as ecosystem engineers through their nest construction activities. They provide macropores for water infiltration (Laundre, 1990; Dean and Yeaton, 1993; Eldridge, 1993; Cerdà and Jurgensen, 2008; Cerdà et al., 2009), mix soil strata (Dauber and Wolters, 2000), may cause the separation of soil particles by size (Frouz and Jilková, 2008), move loose soil to the surface (Eldridge and Pickard, 1994; Lobry de Bruyn and Conacher, 1994), where it becomes available for erosion (Cerdà and Jurgensen, 2008; Cerdà et al., 2009), and change nutrient composition of soil (Dostál et al., 2005), which results in different microorganism communities and enzymatic activity (Pêtal, 1998; Folgarait, 1998; Dauber and Wolters, 2000; Ginzburg et al., 2008; Frouz and Jilková, 2008) and differences in plant growth and nitrogen content (Dean and Yeaton, 1993). Ants also provide gaps for establishment of some plants (Dean et al., 1997; Lenoir, 2009) and disperse certain plant seeds (Azcárate and Begoña, 2007). Through such activities ants contribute to small-scale habitat heterogeneity (Culver and Beattie, 1983; Jouquet et al., 2006). In some aspects their role is similar to that of earthworms and thus increases in importance in drier ecosystems where earthworms are less abundant (Evans et al., 2011).

Ants are also important because of their many direct interactions with other groups. Their role as seed dispersers is of central importance in the Cape Floristic Region (Johnson, 1992). Seed harvesting ants are also abundant in dry areas like the Karoo. Ants also serve as hosts for myrmecophile taxa, are important prey, pollinate some plants, and defend others against herbivores (Hölldobler and Wilson, 1990). Conversely, they can deter pollinators and pest control agents. While many species are generalist scavengers, ants are also major predators of arthropods. Numerous species have mutualistic relationships with plant-sucking insects (Hölldobler and Wilson, 1990). Because they can increase insect pests, much research has focused on managing ants in agricultural systems including in South Africa (e.g. Mgocheki and Addison, 2009, 2010; Nyamukondiwa and Addison, 2011).

3.20.3.1. Taxonomy and collections. Ant taxonomy is comparatively well known. Excellent keys allow genus level identifications with relative ease (e.g. Bolton, 1994). Extant ants are currently classified into 16 subfamilies and 405 genera and subgenera (AntWiki, www.antwiki.org), of which 9 and 71 respectively have been reported for South Africa—including exotics (Fig. 10). However, species-level identification remains difficult for non-specialists. Many informative online resources exist. The web-based keys in B. Taylor's *Ants of (sub-Saharan) Africa* aggregate much of the taxonomic information (www.antsofafrica.org). Taxonomic information, some keys, photos, distribution records and maps, and information on the biology of many species are also available on AntWiki (www.antwiki.org) and AntWeb (www.antweb.org).

Taxonomic changes and outdated keys may confuse non-experts and recent years have seen major taxonomic revisions partially based on DNA analysis. The invasive Argentine ant is sometimes both entered as *Linepithema humile* and with its former name *Iridomyrmex humilis* in reserve species lists. However, excellent resources exist to identify older synonyms (Bolton, 1995, 2003; as well as regular updates to the *Synopsis of the Formicidae* and the *New General Catalogue of the Ants of the World* by B. Bolton on http://www.antwiki.org/wiki/Species_Accounts) and many online sources include recent taxonomic changes as well as synonyms. The Barcode of Life Initiative offers photos, records and DNA sequences (www.boldsystems.org).

Ant research has a long history in southern Africa with early ant taxonomists contributing based on material from local collectors. An early milestone was the work *A monograph of the Formicidae of South Africa* published in several parts by G. Arnold (Arnold, 1915, 1916, 1917, 1920, 1922, 1924, 1926). Arnold also published English translations from much of the early taxonomic literature. More recently the numerous papers by B. Bolton on African ants deserve special notice. Arnold's collection, including many type specimens, is stored at the Iziko South African Museum, whose staff also currently conducts ant taxonomic research involving new collections. In addition to the important ant collection at the South African Museum, there are collections at the Albany Museum, the National Museum, the National Collection of Insects (ARC-PPRI) and the Ditsong National Museum of Natural History. Much

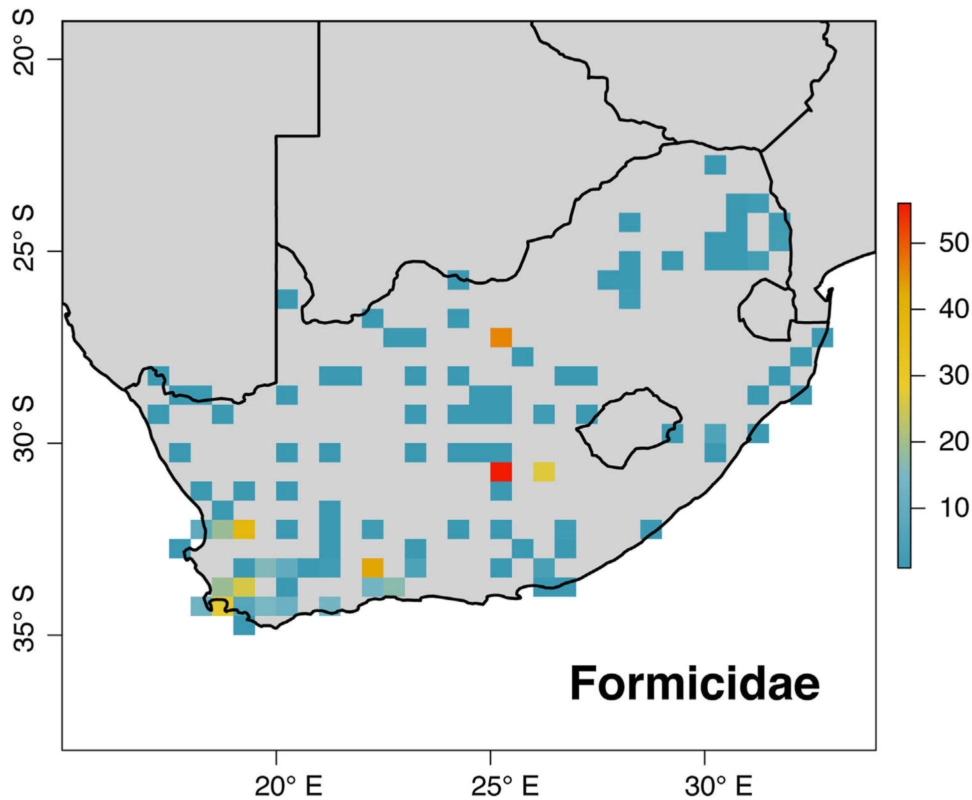

Fig. 10. Species richness distribution for ants in South Africa.

research on African ants past and present has been done by European or American researchers and many collections including South African ants thus exist outside South Africa. Hosting institutions include the Natural History Museum (London, U.K.), the Naturhistorisches Museum (Basel, Switzerland), the Musee d'Histoire Naturelle (Genève, Switzerland), the Museum für Naturkunde der Humboldt-Universitàt (Berlin, Germany), the Natural History Museum (Genoa, Italy) and the California Academy of Sciences (San Francisco, U.S.A.).

3.20.3.2. Sampling and identification. Pitfall traps and baits are widely used, while litter extraction is done using Winkler bags or Tullgren funnels (see e.g. Agosti et al., 2000 for descriptions of methods). Digging may be necessary for strictly subterranean ants, which are otherwise often missed or only recorded from males in light traps. Hand collections or quadrat counts by experts can yield good inventories, but care needs to be taken to standardize the search effort.

3.20.3.3. Invasive species. Invasive ants can have severe impacts, and several alien ant species have been recorded in South Africa. The Argentine Ant (*Linepithema humile*) has raised concern within the Cape Floristic Region as it can disrupt the seed dispersal mutualism (Bond and Slingsby, 1984; Christian, 2001; Christian and Stanton, 2004; Witt and Giliomee, 2004; Witt et al., 2004). Its interference behaviour (De Kock and Giliomee, 1989; Mothapo and Wossler, 2011), effects on other ant species (De Kock and Giliomee, 1989; Schoeman and Samways, 2011), activity patterns (De Kock and Giliomee, 1989), genetic diversity and cuticular hydrocarbons (Lado, 2008; Mothapo and Wossler, 2011), thermal physiology (Jumbam et al., 2008), bait preferences (Nyamukondiwa and Addison, 2011; Vorster, 2011), and effect on distributions of pest insects and their parasitoids (Mgocheki and Addison, 2010) have all been studied.

3.20.3.4. Future research. Many genera, including ecologically important, common and species rich ones, are in urgent need of revision. Researchers frequently encounter species, which cannot be identified with available keys. Robertson (2000) estimated that 45–58% of species in the afrotropical region (including South Africa) are still undescribed or wrongly considered to represent subspecific entities. Revising the genera that have no or outdated keys, will be an important first step toward furthering taxonomic knowledge (Robertson, 2000), with abundant and ecologically important groups treated as priority. Many species remain to be discovered and more needs to be known about the distribution of described species whose ecological niche width may currently be underestimated. Broad-scale standardised surveys should be undertaken and incorporate undersampled areas (in particular the North–West and the Free State). Differences in recorded ant diversity may in part reflect habitats but are likely also caused by differences in sampling effort. Finally, acquiring more information on the biology of ant species and their interactions with other organisms is necessary (e.g. their interactions with fungi and microorganisms, in addition to those with other soil arthropods and with plants).

Recognizing the value of ants for biodiversity monitoring the DST-NRF Centre of Excellence for Invasion Biology has started several ant monitoring programs based on similar methodologies (Botes et al., 2006a; Braschler et al., 2010; Munyai and Foord, 2012; Bishop et al., 2014). One of these – the Iimbovane Outreach Project (www0.sun.ac.za/iimbovane/) monitors ant diversity in pristine and disturbed sites in the Western Cape. It also doubles as a science outreach project communicating biodiversity to teachers and learners of numerous secondary schools by involving them as citizen scientists in the ant diversity research effort (Braschler, 2009; Braschler et al., 2010).

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3.21. Subterranean vertebrates

South Africa has around 1275 species of terrestrial vertebrates (mammals, birds, reptiles and amphibians). Although most of these vertebrate species have minimal direct interaction with the soil, there can be substantial indirect effects. For example, arboreal sunbirds (Family Nectariniidae) have little direct impact on the soil ecosystem, but by the selective fertilisation of plants they excert substantial indirect influences on soil chemical and physical properties. Ecosystem engineers, such as elephants (*Loxodonta africana*), can convert wooded systems to grassland, fundamentally changing the nature and distribution of the soils and the soil biota (Jones et al., 1997; Pringle, 2008). Defecation often has a very local impact on soil fertility and thus affects soil biota. This can be fundamental to soil composition where permanent colonies (birds on offshore islands, bats, etc.) or large short-term aggregations (ungulates on grazing 'lawns') form. Predation on soil biota can influence soil communities (e.g. aardvark *Orycteropus afer* predation on ants and termites), or directly contribute to soil structuring (e.g. hadeda ibis, *Bostrychia hagedash*, aeration of soil by predation on earthworms). A large number of vertebrates also burrow into the soil to build nests (e.g. ground woodpecker, *Geocolaptes olivaceus*), or aestivate (e.g. African bullfrogs, *Pyxicephalus adspersus*). Many (if not most) terrestrial vertebrates, therefore, interact with the soil *sensu lato*. For example, an estimated 28% of squamate reptiles and 10% of amphibians globally can be considered soil-dwelling *sensu lato*, totalling some 2775 species (Measey, 2006). However, here we limit discussion to obligate soil-dwelling South African vertebrates, *viz* the golden moles and mole rats, the amphisbaenians, typhlopids (and selected other snakes) and legless skinks.

Golden moles form a group of 21 species of subterranean mammals that are endemic to sub-Saharan Africa, with the majority of species (17) occurring in South Africa. Golden moles (Chrysochloridae) are unrelated to true moles (Talpidae) or marsupial moles (Notoryctidae), representing a parallel adaptive radiation within the Afrotheria (Madsen et al., 2001; Asher et al., 2010). They are insectivorous, hunting in subterranean tunnels for earthworms, termites and insect larvae, with a wide range of other prey also taken (Fielden et al., 1990; Kuyper, 1985). However, the importance of their activities to the soil environment and prey populations is currently unknown. Golden moles are known to use seismic signals within the substrate for navigation, prey detection and intraspecific communication (Lewis et al., 2006; Narins et al., 1997; Mason and Narins, 2002). Some species have been shown to be highly specialised towards particular soil types, restricting their distribution and also making them vulnerable to population fragmentation through habitat disturbance, especially soil compaction (Jackson et al., 2008a,b). There may therefore be several unknown cryptic species (Jackson et al., 2008b), and many South African species are threatened (IUCN, 2015). Burrows are exclusively temporary in some species (e.g. *Eremitalpa granti*), while others are more permanent (e.g. *Amblysomus hottentotus*) and these can be superficial (breaking the surface) or descending to around one metre in depth (Kuyper, 1985; Rathbun and Rathbun, 2006).

Mole rats (Bathyergidae; four genera and six species in South Africa) include both solitary and eusocial species. They feed principally on underground roots and swollen tubers (Bennett and Jarvis, 1995), and the over-dispersed distribution of species in arid areas is thought to have contributed to the evolution of eusociality in this group (see Bennett and Faulkes, 2000). Despite the disproportionate attention that this group has received in behavioural, ecological and physiological sciences, the taxonomy is not fully resolved, and several cryptic species await description (Faulkes and Bennett, 2013).

Amphisbaenians or worm lizards are a group of limbless burrowing lizards (*Lacertilia*) with a principally Gondwanan distribution. The South African fauna consists of some ten species in four genera distributed for the most part in northern areas with sandy soils (Measey, 2014). Good collections of specimens are in the Port Elizabeth Museum, the National Museum and the Ditsong National Museum of Natural History. Both atlas records (Bates et al., 2014) and keys (Branch, 1998) are readily available for South Africa. Amphisbaenians superficially resemble earthworms, with rings of scales encircling the body, and their head shape is adapted for their obligate burrowing lifestyle. They are all predators of soil invertebrates, typically termites, and prey is usually swallowed whole (Webb et al., 2000). Individuals are normally only encountered when large quantities of soil are moved, or when areas become flooded in extreme weather events. Few techniques have been proposed for their sampling, although Measey (2006) and Measey et al. (2009) suggested digging quadrats for quantitative sampling of *Zygaspis vandami*. Branch (2006) called for the phylogenetic resolution of this group as a priority (but see Measey and Tolley, 2013) and taxonomic work at species level is ongoing. The ecological impact of these species on soil biota and soil structure is currently unknown. Some species are known to occur at substantial depths in the soil profile and are known to be able to generate considerable burrowing forces (Navas et al., 2004). Pooley et al. (1973) reported surprisingly high densities, but Measey et al. (2009) failed to find comparable densities in the same areas 35 years later, prompting concerns about their current conservation status. The conservation status of amphisbaenians is largely unknown, with 50% of species being classified as Data Deficient (Böhm et al., 2013). The dispersal ability of amphisbaenians is currently unknown, and this will likely be important in consideration of the conservation status. The subspecies *Chirindia langi occidentale* from the Soutpansberg is considered Vulnerable due to its small area of occurrence and the impact of soil compaction by livestock (Measey, 2014).

The scolecophidians are an infraorder of snakes known as 'blind snakes' which have the centre of their distribution in areas which formerly made up Gondawanaland. Typhlopids (Typhlopidae and Leptotyphlopidae) are a diverse group of small and large bodied snakes with extremely conserved morphology, making their identification problematic. There are three genera and 23 species in South Africa (Measey and Branch, 2014), as well as the introduced (and panglobal) parthenogenetic flowerpot snake, *Ramphotyphlops braminus*. The smallest species are not larger than a typical earthworm (up to 180 mm, *Typhlops fornasini*), while the largest blind snakes (e.g. *Megatyphlops mucruso* and *M. schlegelii*) can reach over 1 m in length. All species prey on ants and termites (often just the brood), which are raked in large numbers using modified jaws (see Kley, 2001; Webb et al., 2000). Good collections of individuals are in the Port Elizabeth Museum, the National Museum and the Ditsong National Museum of Natural History. Both atlas records (Bates et al., 2014) and keys (Branch, 1998) are readily available for South Africa. Despite their lack of distinguishing morphological features, the taxonomy and phylogenetic relationships of scolecophidians are generally well resolved (e.g. Vidal et al., 2010; Broadley and Wallach, 2009). However, their impacts on the soil ecosystem are unknown. Globally, like the amphisbaenians, many species of blind snakes (49% and 40%, respectively) are considered to be Data Deficient (Böhm et al., 2013), but in South Africa none are considered threatened (Measey and Branch, 2014).

In addition to the blind snakes, South Africa has a number of other burrowing snakes: mole snakes (genus *Pseudaspis*), shovel-snouted snakes (genus *Prosymna*), and African burrowing snakes (Family Atractaspidae; genera *Atractaspis*, *Aparallactus*, *Amblyodipsas* and *Xenocalamus*). The very common and widespread mole snake (*Pseudaspis cana*) spends much of its time underground where it principally preys on golden moles and mole rats. The largest of the burrowing snakes, mole snakes are probably the most important predators of subterranean mammals in South Africa, and reach high densities where their prey is abundant. Five species of shovel-snouted snakes occur in South Africa, all of which burrow in loose soil in search of reptile eggs, which they swallow whole (Branch, 1998). In South Africa, the two species of *Atractaspis* and three species of *Amblyodipsas* typically take small lizards and frogs sheltering in the soil, while the two *Aparallactus* species are principally consumers of centipedes. The three species of *Xenocalamus* in South Africa are of particular interest as they are thought to feed almost exclusively on amphisbaenians (Branch, 1998; Shine et al., 2006). The biology of all of these burrowing snakes is very poorly known, together with their distribution and impact on the soil ecosystem in which they probably represent top predators.

South Africa has an impressive diversity of legless (or near limbless) skinks. There are two major groups: the African legless skinks (Acontinae) and the Old World skinks (Scincinae). They are a particularly colourful group of subterranean reptiles, many with stripes, and often with brightly coloured tails: pinks, blues, yellows and reds are all common colours, which are also known in the subterranean caecilians (Wollenberg and Measey, 2009). Most acontines are restricted to the topsoil of their preferred sandy substrates (genus *Acontias*, eight species, genus *Typhlosaurus*, eight species, genus *Acontophiops*, one species). The dwarf burrowing skinks (genus *Scelotes*, 17 species) include both limbed and limbless individuals. These animals are usually small and burrow superficially in sandy substrates. The taxonomy of both of these groups is in flux and there are likely to be many cryptic species as well as new species as yet uncollected (see for example Engelbrecht et al., 2013; Heideman et al., 2011).

Burrowing imposes severe constraints on locomotion as it has high energetic costs which have been quantified for some fossorial vertebrate taxa (e.g. amphisbaenians: Navas et al., 2004; golden moles: Seymour et al., 1998; mole rats: Lovegrove, 1989; caecilians: Herrel and Measey, 2010). In addition to these high energetic costs, prey can be particularly sparse in the subterranean environment of arid areas where many of the South African species occur. This appears to result in a heavy reliance by many of these vertebrate predators on social soil macroinvertebrate prey items, which represent over-dispersed distributions with locally high prey concentrations and large rewards in terms of energy. However, the impact of these diverse obligate South African soil vertebrates on the same prey items, which themselves are soil ecosystem engineers, has not been studied. Several species of mole rats, and even some golden moles, are recognised as pests in domestic lawns and other grassy areas. There they presumably feed on invasive earthworms, raising the question of how the expansion of urban habitats and their associated invasive soil macroinvertebrates has facilitated range expansion in golden moles. Range expansion of urban exploiters such as hadeda ibis has been shown to be linked to the spread of human-modified habitats (Duckworth et al., 2012).

4. Discussion

4.1. Estimates of current diversity and sampling gaps

We estimate that over 24,000 species of soil animals and 651 fungal species have been described in South Africa. This means that ~1.8% of the world's soil biota is known from South Africa (Table 1), a country which represents only 0.8% of the earth's terrestrial area. However, there is no sign of a decline in the rate of new species descriptions. From 1963–2012, i.e. the last 50 years, the rate of descriptions of new soil animal species has been fairly constant (average of 20.5 described per year, range 2–77; Fig. 2). Given there are substantial gaps in sampling for even well studied groups, it is clear that the real below-ground diversity will be much larger than current estimates.

Our predictions of high soil faunal species richness and endemism fits with South Africa's reputation as a region of exceptional biodiversity (Mittermeier et al., 1999). Of all taxonomic groups assessed in this review, South African Embioptera have the largest proportion of global taxa with 10.28% of all known species recorded in South Africa, followed closely by the Scarabaeinae (8.47%), earthworms (7.73%), scorpions (6.75%) and the nematodes (6.40%). However, taxa that show a low global representation (<1% in Table 1) are probably poorly known (e.g. there is no current local taxonomic expertise for groups such as proturans, Pauropoda, Symphyla and Enchytraeidae), or are under sampled (e.g. Tardigrada, Diplura, Collembola). Endemicity in South African soil biota is above 50% for most groups, and particularly high for bristletails (90%), gastropods (80%), mites (~80%), isopods (95%), millipedes (80%), Opiliones (92%), pseudoscorpions (70%) and entomopathogenic nematodes (73%) (Table 1). However, these high levels of endemicity are likely in part due to the paucity of records from neighbouring countries (Botswana, Lesotho, Mozambique, Namibia, Swaziland and Zimbabwe). More sampling across the sub-region is required to confirm the exact extent of endemism.

While South Africa is clearly a megadiverse country both above ground (e.g. Hockey et al., 2005; Skinner and Chimimba, 2006) and below ground (Table 1), foundational biodiversity knowledge is lacking for most South African soil biota. Some groups and areas have been well sampled, but sampling has largely been group-specific and research has often been directed to taxa with socio-economic impacts. The majority of sampling has been in relatively small areas of the country close to the major population centres. There are large, inland areas of heavily utilised soils without any diversity data (Fig. 11). Even for extensively studied groups such as spiders and gastropods, sampling gaps still exist. Sampling areas that have been poorly studied should be a priority for future work.

4.2. Conservation

Global conservation assessments have been conducted on a limited number of taxonomic groups, but even within these, soil-dwelling species are disproportionately classified as Data Deficient in the IUCN red list criteria (e.g. Gower and Wilkinson, 2005; Böhm et al., 2013). This appears to be related to the limited number of soil biota researchers; difficulties in identification due to the high level of conserved morphological features across phylogenies; and inherent logistic difficulties in surveying and sampling. Even the most basic IUCN Red List criteria require a reasonable understanding of the taxonomy and distribution of individual species. Our results agree with previous findings that many taxonomic groups of soil biota could not be assessed for conservation status due to a lack of baseline data. However, exceptions do exist, and the recent *First Atlas of the Spiders of South Africa (Arachnida: Araneae)* (Dippenaar-Schoeman et al., 2010) provides an excellent model of what is possible.

Despite their abundance and importance in soil function shown elsewhere (Bardgett and Wardle, 2010; Bardgett and van der Putten, 2014), soil fauna are rarely used as indicators of soil health in South Africa (though see McGeoch et al., 2011, for the use of ants, and McGeoch et al., 2002, for the potential of using beetles). Although endemic species, such as molluscs and dung beetles have been used as indicators of diversity in South Africa (van Jaarsveld et al., 1998; Kryger et al., 2006; Uys et al., 2010), the inclusion of other endemic soil biota in conservation planning should be the

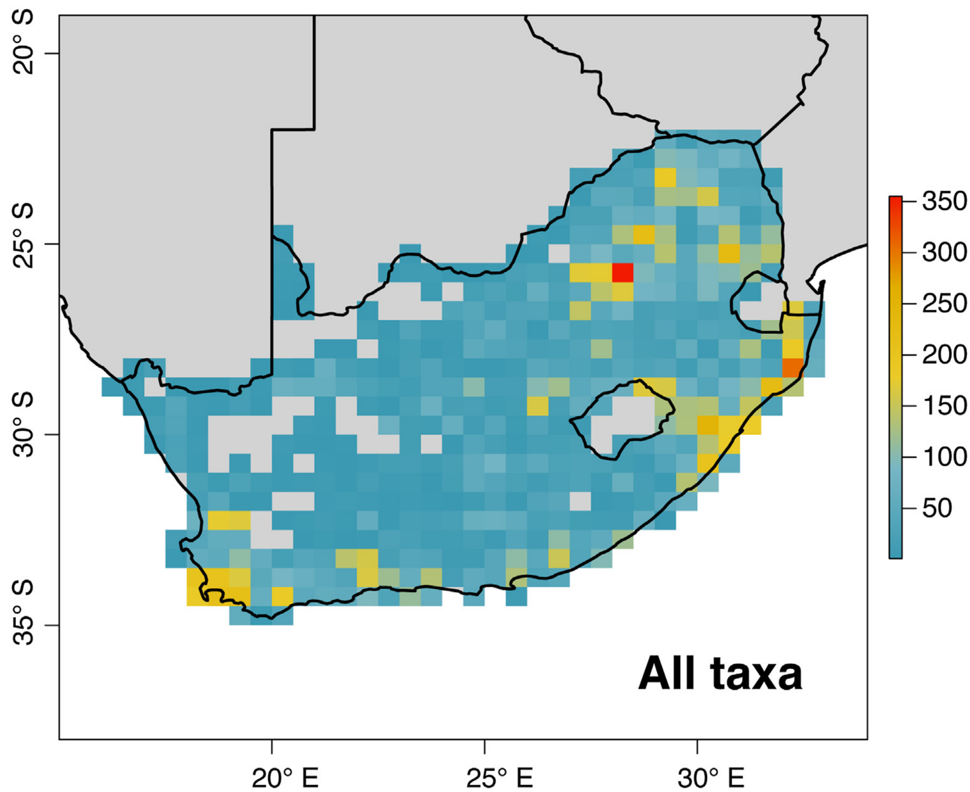

Fig. 11. Taxonomic unit richness map for all South African soil fauna discussed in this study.

next step to ensure soil habitat conservation. The use of invertebrates as biological indicators in South Africa has been reviewed (McGeoch, 1998), and recommendations on their implementation have been made (see McGeoch et al., 2002, 2011). Indeed, a recent review by Gerlach et al. (2013) suggested ants, millipedes, harvestmen and gnaphosid spiders should be used as potential bioindicators, and argued that taxonomy and species identification pose the major hurdle for using other soil fauna. These problems may be overcome by focusing on the research gaps identified in this review, after which a soil biodiversity monitoring framework can be initiated as has been successfully done on a large scale in Europe (Faber et al., 2013; Gardi et al., 2009).

4.3. Threats

It has been suggested that modifications of soil biota communities, especially in terms of soil macrofauna, results in the functional loss of crucial regulatory mechanisms (Lavelle et al., 1994; Bardgett and van der Putten, 2014). Global drivers, such as land degradation, exploitation, pollution, climate change and biological invasions, are a serious threat to global biodiversity (MEA, 2005), including South Africa's (Chown, 2010). The number of invasive species present in soil is relatively well known for many well-studied and conspicuous groups such as the earthworms, isopods and gastropods (Plisko, 2001, 2010; Herbert, 2010; Picker and Griffiths, 2011). A cause for concern, however, is that there are few data on the distributions of invasive taxa, and almost no research on the impacts of invasions on indigenous species or ecosystem services. For less well-studied groups the presence of invasive species has not even been determined. Moreover, determining whether taxa are native or alien can often be problematic, though DNA barcoding techniques can assist in this endeavour (for examples on Collembola and earthworms see Janion et al., 2011; Porco et al., 2012; Decaëns et al., 2013).

The identification and assessment of distributions of invasive species should become a research priority for all soil biota groups, especially when considering that climate change will likely directly and indirectly favour invasive species in other South African ecosystems (Irlich et al., 2014). This should be true not only in disturbed areas, but also in protected areas, as recent evidence showed that national parks in South Africa are experiencing significant increases in temperature and changing rainfall patterns (van Wilgen et al., 2016). The movement of soil, which acts as carrier medium for fauna and flora, has been a major historical pathway of human-mediated introduction and translocation of organisms throughout the region (MacDonald et al., 1986). It is less clear, however, whether a lack of dispersal would limit invasions spreading into undisturbed soils, but evidence from protected areas (see cases above) is worrying. The impacts of these invasions on ecosystem functioning are not currently known, although research suggests that invasive plants reduce the diversity of insect species (Steenkamp and Chown, 1996; Samways et al., 1996; Coetzee et al., 2007) and may also impact the soil microbial community through soil chemistry changes (Slabbert et al., 2010, 2014; Souza-Alonso et al., 2014).

Other threats to soil biota include soil erosion, soil compaction and soil organic matter decline (Gardi et al., 2009). In particular, intensified land-use is a threat to soil biodiversity globally (Tsiafouli et al., 2015), and in South Africa (Scholtz and Chown, 1993). The livelihoods of people in South Africa depend in many ways on the continued functioning of the soil ecosystem, so there is an urgent need for basic biodiversity knowledge in order to facilitate the soil ecosystem research required to assess sustainability (Louw et al., 2014).

4.4. Integrative sampling and recommendations

There are clearly some commonalities in how soil biota have been sampled. Tullgren funnels are used to obtaining quantitative sampling data for about a third of groups, while pitfall traps are used to collect almost half of the groups considered here. However, more labour-intensive and time-consuming sampling methods (including digging for deep euedaphic species, such as earthworms, and active searching for many groups such as arachnids and molluscs) are often required. The collection methods adhere to the ISO (International Organization for Standardization, www.iso.org) guidelines and accepted soil assessment sampling methods (Römbke et al., 2006a). With a combination of different sampling techniques and the application of the relevant extraction methods targeting specific taxa, several additional soil biota groups can be collected rather than one target group as is usually done. This will enable bycatch to be sorted into different taxa and assigned to relevant taxonomists and museum collections (Table 1). Most of the collection or extraction methods do not require intensive training, are relatively inexpensive, and thus can be implemented by non-experts. Sorting into major groups can be done and samples distributed to experts (Fig. 12). An integrative sampling approach to acquiring foundational knowledge of soil biodiversity may be especially relevant due to the interdependencies of organisms at different scales (Lavelle et al., 1994; Faber et al., 2013; Bardgett and van der Putten, 2014). Holistic approaches such as these have been successfully undertaken in large-scale non-soil projects in South Africa, such as recent work on estuaries (van Niekerk et al., 2013). For soil fauna, comprehensive projects such as BISQ (Rutgers et al., 2009) and EcoFINDERS (Faber et al., 2013) have formed excellent models of coordinated research sampling, soil monitoring schemes and indicator species selection. Recently, Ramirez et al. (2015) proposed a global soil biodiversity information platform, which is an effective way to encourage interdisciplinary work, share knowledge and manage data.

4.5. Moving forward

Africa has the lowest number of papers describing new species compared to other parts of the world (Costello et al., 2013). To rectify this in South Africa, the Soil Ecosystem Research Group (SERG, www.sergsa.org) aims to collate as much existing soil biology information and to describe as many new soil and litter associated species as possible. Actions to increase the number of species descriptions suggested by Costello et al. (2013) should be applied in South Africa. Most importantly, coordinated sampling and knowledge sharing through this existing network of specialists will greatly enhance our productivity, whilst the extended network through our global partners should facilitate training of more taxonomists and attract more researchers to southern Africa. Recommendations for improved data collection, storage and dissemination of soil information have recently been made by South African soil scientists (Paterson et al., 2015), and thus perhaps a closer integration of soil related disciplines are needed. Funding needs to be put in place to: (i) train taxonomists; (ii) Consolidate and curate existing collections for improvement of data storage and management (Hamer, 2012); (iii) Capture existing data; (iv) Fill gaps identified in this paper, especially focusing on the functional roles of soil biota; (v) Use our existing and growing expertise as a base to tackle a continental deficiency in our understanding of soil ecosystems; and (vi) Use current taxonomic expertise to facilitate the development of DNA barcode libraries. These will aid South Africa, at least in terms of soil biodiversity, to meet some of the Aichi Biodiversity Targets (Unep, 2011) and address the Global Taxonomy Initiative (GTI) as part of the Strategic Plan for Biodiversity of the Convention on Biological Diversity (www.cbd.int).

4.6. Conclusions

South Africa contains nearly 2% of the world's described soil species, with high local endemicity. However, most groups are

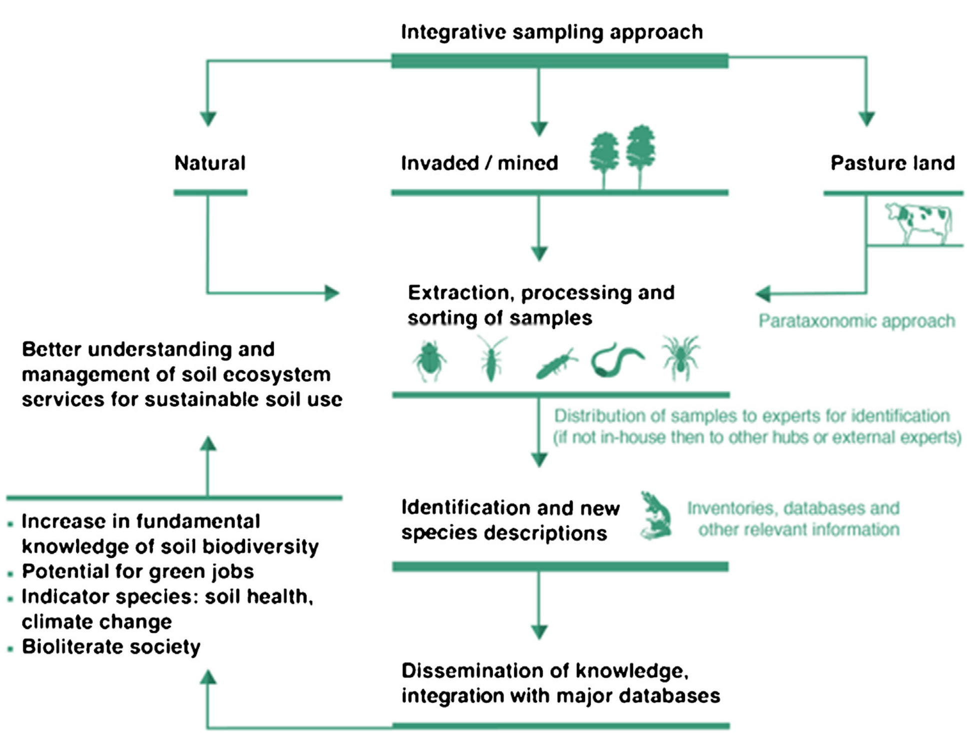

Fig. 12. A schematic example of an integrative sampling approach.

under sampled and in need of revision (Table 1). South Africa can already be described as a megadiverse country for soil fungi and fauna, but we are not yet aware of the full scope of this diversity. We conclude that ideally, a conservation and management plan for South African soil organisms would include: (i) identification of threatened soil systems; (ii) the ability to identify invasive threats to soil health; (iii) identification of groups which would be good indicators of soil health for monitoring purposes; and (iv) manage components of soil biota to maintain and improve ecosystem services. Until these strategies are in place, the conservation of threatened ecosystems and landscapes should be a priority.

In South Africa, funding and expertise is required in a coordinated research framework. Successful examples of this approach have been demonstrated for Europe, such as BISQ (Rutgers et al., 2009) and EcoFINDERS (Faber et al., 2013), while the Global Biodiversity Soil Initiative (GBSI, http://www.globalsoilbiodiversity.org/) is an excellent platform for interaction with the wider research community and to generate knowledge transfer. The development of an integrative sampling approach to sampling soil communities (Fig. 12) should be initiated in South Africa to place taxonomic knowledge in an ecological context (see Sutherland et al., 2006; Pretty et al., 2010) and develop monitoring tools to provide valuable advice for soil health management. Such an overall strategy for South African soil biota research is needed, which recognises that although different research priorities exist for each group, sharing and contrasting experiences will help advance our knowledge across the board. We see the formation of SERG as the first of many steps towards the goal of an integrative approach to soil ecosystem research in South Africa.

Conflict of interests

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pedobi.2016.03.004.

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