Springtail Diversity in the Cape Floristic Region

by

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Abstract

Understanding the distribution, abundance and diversity of species and the mechanisms causing these patterns has been the interest of ecologists and taxonomists for decades. The exceptionally high plant diversity in the Fynbos biome has been well studied. Whilst early arguments suggested that the high plant diversity is not reflected in the arthropod diversity and that insect species richness is low compared to other comparable areas, these observations might have been hampered by the taxonomic impediment. Despite global recognition of the significance of this below-ground component of diversity for ecosystem functioning, soil is one of the most poorly studied habitats of terrestrial ecosystems. Although knowledge is increasing for epigaeic groups, other significant groups such as the Collembola remain especially poorly understood. This thesis starts addressing this serious gap in knowledge concerning the below-ground component of biodiversity in the Fynbos biome and the effects of landscape transformation thereon. As part of the work, considerable attention was given to resolving the taxonomic impediment for the springtail fauna of the Fynbos biome using modern morphological and DNA barcoding methods, while also examining the correlates of soil animal diversity in the biome, by using Collembola (springtails) as exemplars. First, using a combination of published records of Collembola from South Africa, various sampling methods and DNA barcoding, a species list is compiled for the Western Cape. Currently 213 species are known to exist from the Western Cape. A high level of cryptic diversity was also found in several genera, together with several potential species radiations in the *Ectonura*, *Seira*, *Parisotoma* and *Cryptopygus*. A start is a made at addressing the lack of taxonomic knowledge by describing five new species. Two *Ectonura* Cassagnau 1980 species are described from Betty's Bay and Grootvadersbosch respectively and a key to the Neanurinae of South Africa is provided. The first record of the genus *Triacanthella* Schäffer, 1897 is described from a cave in Table Mountain, while two new species of *Delamarephorura* are described and the genera *Spicatella* Thibaud 2002 and *Delamarephorura* Weiner & Najt 1999 are synonymized. Although fire is thought to be the main form of decomposition in the Fynbos biome, recent work has shown that biological decomposition may be more important than previously thought. I examine the resilience of Collembola after a large-scale fire in Jonkershoek Nature Reserve using quantitative sampling which is temporally replicated. The resilience of invertebrate fauna in the fynbos is not well understood, thus I investigate the diversity of Collembola before and after a major fire. Results show Collembola species richness and abundance recovered surprisingly quickly after the fire. On a larger scale, litterbags were deployed at six sites across the Western Cape using different litter types. Here, a total of 113 morphospecies species was found. Local richness was found to be highest in Kogelberg (32 species), while the turnover between sites was also high. Thus, the degradation of local habitat patches will be as much of a threat to Collembola as to the endemic plants in this region.

Opsomming

Begrip van die verspreiding, spesierykheid en verskeidenheid van spesies en die meganismes wat hierdie patrone veroorsaak is al die belangstelling van ekoloë en taksonome vir dekades. Die buitengewoon hoë plant diversiteit in die Fynbos-bioom is goed bestudeer. Terwyl vroeë argumente voorstel dat die hoë plantdiversiteit nie weerspieël word in die geleedpotige diversiteit nie en dat insekspesierykheid laag is in vergelyking met ander gebiede, kon hierdie waarnemings nie gemaak word nie as gevolg van taksonomiese hindernisse. Ten spyte van die wêreldwye erkenning van die belangrikheid van hierdie ondergrondse komponent van diversiteit vir die funksionering van die ekosisteem, is die grond een van die swakste bestudeerde habitatte van terrestriële ekosisteme. Alhoewel kennis vermeerder vir bogrondse groepe, word ander belangrike groepe soos die Collembola swak verstaan. Hierdie tesis begin hierdie ernstige leemte in kennis aanspreek, met betrekking tot die ondergrondse komponent van biodiversiteit in die Fynbos bioom en die gevolge van die landskap transformasie daarop. As deel van die werk, is heelwat aandag gegee aan die oplossing van die taksonomiese hindernis vir die springstert fauna van die fynbos bioom met behulp van moderne morfologiese en DNA metodes, terwyl dit ook die ooreenkomste van grond diere diversiteit ondersoek in die bioom, deur gebruik te maak van Collembola (springsterte) as voorbeelde. Eerste, met behulp van 'n kombinasie van gepubliseerde rekords van Collembola van Suid-Afrika, verskillende kolleksie metodes en DNA metodes is 'n spesielys saamgestel vir die Wes-Kaap. Tans is 213 spesies bekend vir die Wes-Kaap. 'n Hoë vlak van kriptiese diversiteit is ook gevind in verskeie genera, saam met verskeie potensiële spesies radiasies in die *Ectonura*, *Seira*, *Parisotoma* en *Cryptopygus*. 'n Begin is gemaak op die aanspreek van die gebrek van taksonomiese kennis deur vyf nuwe spesies te beskryf. Twee *Ectonura* Cassagnau 1980 spesies van Bettiesbaai en Grootvadersbosch is beskryf en 'n sleutel tot die Neanurinae van Suid-Afrika word verskaf. Die eerste rekord van die genus *Triacanthella* Schaffer, 1897 word beskryf van 'n grot in Tafelberg, terwyl twee nuwe spesies van *Delamarephorura* beskryf word en die genera *Spicatella* Thibaud 2002 en

Delamarephorura Weiner & Najt 1999 gesinomiseer word. Hoewel vuur beskou word as die belangrikste vorm van ontbinding in die Fynbos bioom, het onlangse werk getoon dat die biologiese ontbinding belangriker mag wees as wat voorheen vermoed was. Ek ondersoek die veerkragtigheid van Collembola na 'n groot skaal vuur in Jonkershoek Natuurreservaat met behulp van kwantitatiewe steekproefneming wat tydelik herhaal. Die veerkragtigheid van ongewerwelde fauna in die fynbos word nie goed verstaan nie, dus het ek ondersoek ingestel na die diversiteit van Collembola voor en na 'n groot vuur. Resultate toon dat Collembola se spesierykheid en hoveelheid verbasend vinnig herstel na die vuur. Op 'n groter skaal, is kolleksies by ses plekke regoor die Wes-Kaap gebruik en verskillende blaarafval word vergelyk. Hier word 'n totaal van 113 morfologiese spesies gevind. Daar is gevind dat die hoogste aantal spesies in Kogelberg is (32 spesies), terwyl die omset tussen plekke baie hoog was. So sal die agteruitgang van plaaslike habitatte net soveel van 'n bedreiging inhou vir Collembola as vir die endemiese plante in hierdie streek.

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Appendix 5	Bengtsson, J., Janion, C., Chown, S.L. and Leinaas, H. P. (2012) Litter decomposition in fynbos vegetation, South Africa. *Soil Biology & Biochemistry* **47**, 100-105.

Chapter 1

General Introduction

"The tiny creatures of the undergrowth were the first creatures of any kind to colonise the land. They established the foundations of the land's ecosystem (and) were able to transcend the limitations of their small size by bonding together in huge communities of millions. If we and the rest of the back-boned animals were to disappear overnight, the rest of the world would get on pretty well. But if the invertebrates were to disappear the land's ecosystems would collapse. Wherever we go on land, these small creatures are within a few inches of our feet – often disregarded. We would do well to remember them". - David Attenborough.

Biodiversity: "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" - Heywood 1995

Biodiversity in South Africa

Large-scale patterns in biodiversity are well understood for plants (Currie & Paquin 1987, Francis & Currie 1998, Hillebrand 2004, Wilson et al. 2012) and vertebrate groups (Currie 1991, Davies et al. 2007, Gonzalez-Voyer et al. 2011, Safi et al. 2011, Jetz & Fine 2012, Gaston et al. 2007, Thomas et al. 2008). For South Africa, similar patterns have been investigated for major taxa, such as mammals, birds and plants (Huntley 1989, Andrews & O'Brien 2000, van Rensburg et al. 2002, Chown et al. 2003, Thuiller et al. 2006, 2007, Mokhatla et al. 2012), with energy being a major predictor of species richness patterns. In addition, some smaller scale variation in biodiversity has been investigated, especially the influence of habitat transformation such as fire, climate change and invasive species on local species richness (van Wilgen et al. 1992, Midgley et al. 2002, Evans et al. 2006, Richardson et al. 2005, Gaertner et al. 2009). In contrast, the biodiversity patterns for insects in South Africa are only beginning to be elucidated. These studies focus mainly on taxonomically well-known groups such as ants (Parr et al. 2005, Botes et al. 2006, Braschler et al. 2012) and beetles (Davis 1997, Davis et al. 1999, Botes et al. 2007). Again, energy variables largely explain the species richness patterns found. A few exceptions are notable, such as the high plant diversity in the fynbos biome (Kreft & Jetz 2007). For insects, monkey beetles (Scarabaeidae) show high beta diversity in the Succulent Karoo which is correlated with high plant beta diversity (Colville et al. 2002).

Despite the significant contribution of soil fauna to above-belowground diversity and ecosystem functioning (Wardle 2002, Wardle et al. 2004, Bardgett & Wardle 2010), the soil fauna is especially poorly understood for South Africa. Although pioneering work was undertaken by Lawrence (1953), knowledge of soil fauna is largely restricted to taxonomically well-known groups such as ants (Robertson 2000, 2002, Parr et al. 2003), some mite groups (Roets et al. 2006, Ermilov & Hugo-Coetzee 2012) and earthworms (Plisko 2010). Recently Plisko (2010) highlighted the fact that although the earthworms are relatively well known for South Africa (due to good taxonomic expertise), the number and effect of invasive species on the native fauna is not well known. Collembola are amongst the least known groups of soil fauna in South Africa, with the last comprehensive work undertaken nearly fifty years ago by Coates (1968a, b).

Collembola (commonly known as springtails) are an ancient group of arthropods more closely related to Crustaceans than to insects (Nardi et al. 2003). Together with mites (Acari) Collembola make up 90% of the micro-arthropod population in soils and play a fundamental role in terrestrial ecosystem functioning (Hopkin 1997, Rusek 1998). Collembola can occur in numbers ranging up to millions of individuals per m^2, and are found in almost every part of the world, from deserts to the Arctic and Antarctic, from coasts to the highest peaks (Rusek 1998). They are often grouped into three large categories or life forms, namely epedaphic (surface-dwelling), hemi-edaphic (litter dwelling), and euedaphic (soil dwelling) (Gisin 1943). Collembola feed on a variety of organisms including Protozoa, Nematoda, Trematoda, Rotifera, invertebrate carrion, plant litter, live roots and bacteria, algae, fungi, and microorganisms on plants roots and on leaf litter (Hopkin 1997, Rusek 1998). Furthermore, they form the prey of many animals, including spiders, beetle larvae, predatory mites, dipterans, ants, other Collembola, and even frogs and reptiles (Rusek 1998). Collembola can play a major role in forming soil microstructure in weakly developed soils, either by actively making micro-tunnels in the soil, or by their frass contributing to humus formation (Rusek 1985). Soil organisms can affect plants directly and indirectly by providing nutrients, mutualistic relationships and by feeding on harmful pathogens (Wardle et al. 2004). Furthermore, soil animals can indirectly affect plant consumers (Wardle et al. 2004).

Soil organisms such as Collembola have proven to be useful model organisms (Hopkin 1997, Ettema & Wardle 2002, Rusek 1998). Collembola respond to a variety of environmental factors, and are well represented in the soil in terms of diversity (Hopkin 1997, Sousa et al. 2006). Hence, Collembola are widely used in biodiversity assessments, ecotoxicology studies and as indicators of soil health and pollution (Hopkin 1997, Cassagne et al. 2006). This group has also been proven useful as an indicator of ecosystem disturbance, especially the use of endemic species (Deharveng 1996, Cassagne et al. 2006). Endemic species often represent a large proportion on the total assemblage (Deharveng 1996) and are thought to be more vulnerable to loss of natural habitat than non-endemic species. Thus, they can be used to assess the effect of environmental change and habitat disturbance (Cassagne et al. 2006).

Furthermore, Collembola have proven useful to investigate the effects of climate change (Kennedy 1994, Coulson et al. 2000, Sinclair & Stevens 2006) and the interaction between climate change and biological invasions (Chown et al. 2007, Slabber et al. 2007).

Collembola diversity at different spatial scales

Local diversity patterns

As mentioned, Collembola can occur in most microhabitats throughout the world. Density measures has been estimated to range from as low as 100 individuals m^{-2} from a desert in California (Wallwork 1972), up to 670 000 individuals m^{-2} at Signy Island, Antarctica (Collins et al. 1975, see Peterson & Luxton 1982). Similarly, species richness can range from three species (also from the desert, Wallwork 1972) to 48 species in an Irish bog (Blackith 1974). Generally, polar or desert habitats have low numbers of species, while forests and temperate deciduous forests are thought to be rich. However, in comparison to other parts of the world, data from tropical forests are lacking (Petersen & Luxton 1982). For South Africa, only one study systematically documenting the alpha diversity of Collembola exists. Liu et al. (2012) found a total of 34 morphospecies in the endangered Cape Flats Sand Fynbos, while 42 species were found in the neighbouring pine plantations. There was a positive relationship between site humidity and Collembola richness and abundance. However, more introduced species were found in the pine plantations than in the fynbos.

Regional and global diversity patterns

Understanding the diversity patterns of soil animals is important to understand how they will respond to global change, and in turn affect the delivery of ecosystem services (Lavelle et al. 2006). It has been shown that a macro-ecological approach may be useful to examine large-scale patterns of soil fauna species richness and abundance (Petersen & Luxton 1982, Ulrich & Fiera 2009, 2010). For Collembola, species richness declines towards the poles, whilst body size increases (Petersen & Luxton 1982). More recently, Ulrich & Fiera (2009) examined the spatial distribution of 2102 species of Collembola from 52 countries. They illustrated that area, winter length, and annual temperature difference are major predictors of European Collembola species richness. There was also a clear latitudinal trend, with species richness increasing with an increase in latitude. In a meta-analysis study, Blankinship et al. (2011) used data from global change manipulation experiments to investigate the effect increased levels of CO_2, temperature and changing rainfall patterns will have on soil organisms. In general, increased warming and precipitation showed a positive effect size which intensified with time, while abundance increased with an increase in CO_2. These patterns need further investigation using more groups of soil fauna, as large-scale investigations of these taxa are lacking (Decaëns 2010).

Vegetation can have an impact on the diversity of soil biota by means of litter production affecting the soil system (Wardle 2002). This has been shown experimentally, where mite species richness and abundance showed an increase in mixed-species litter bags compared with single-species litter bags (Kaneko & Salamanca 1999). However, it has been suggested that litter quality is more important than litter quantity (Salamon et al. 2004). More comparative studies are necessary before any generalisations can be made. Collembola are a useful group to test if this pattern holds for a group that consist of both litter and soil dwelling species.

Several environmental factors have been investigated that may drive patterns of soil biodiversity. Soil properties, vegetation characteristics and interspecific interactions are factors thought to drive the spatial variation in soil biodiversity (Decaëns 2010). Other authors also found climate and soil properties such as pH and moisture to be important in structuring Collembola communities (Gabriel et al. 2001, Raschmanová et al. 2008, Salamon & Alphei 2009). A positive relationship between habitat heterogeneity and species richness has also been found for Collembola (Sousa et al. 2006, Vanbergen et al. 2007). In plantations, higher Collembola abundances have been associated with the decompositional properties of the environment, including higher moisture content and C:N ratios of leaf-litter and soil (Robson et al. 2009). In the Antarctic however, historical geological events could explain the distribution of certain Collembola species (Caruso et al. 2009).

Understanding species richness patterns is important to understand how soil animals will respond to global change, and in turn affect the delivery of ecosystem services (Lavelle et al. 2006). It is evident from the examples above why there has been a global interest in soil fauna, as they have proven to be particularly useful model organisms, and may also be used in such a way in South Africa. In addition, the question whether local or regional processes are driving the patterns observed can be addressed.

The Cape Floristic Region

Plant and arthropod diversity

The Cape Floristic Region (CFR), is considered one of only six floristic kingdoms of the world, and is widely known as a hotspot for vascular plant biodiversity (Myers et al. 2000, Mittermeier et al. 2004). This area of approximately 90 000 km^2 contains almost 9 000 species of flowering plants, of which 6 210 are endemics (Cowling et al. 1992, 1996, Goldblatt & Manning 2002, Rebelo et al. 2006). Fynbos, defined as the vegetation type dominated by proteoids, ericoids and restioids, is the dominant vegetation type in the CFR. Plant endemism is calculated to be 68% for species and 20% for genera (Goldblatt & Manning 2002). The Cape Peninsula is especially well investigated and is species rich, with 2 285 species of native plants in 471 km^2 (Helme & Trinder-Smith 2006).

The high richness of plant species is thought to have resulted from limitations to gene flow (landscape barriers, pollinator and phenological specialisations) as well as a highly variable geography and climate resulting in the extreme radiation of the Cape flora (Linder 2003). Various biotic and abiotic variables have been investigated to explain the patterns of plant species richness in the CFR. Environmental factors such as precipitation, vegetation type, substratum and altitude have been suggested as correlates of plant species richness in the CFR (Goldblatt 1978, Linder 1991, Dupont et al. 2011). Linder (1991) found that plant species richness in the CFR was best predicted by total precipitation. Historical climatic factors and high levels of beta and gamma diversity can explain the diversity of plants found in the south-west compared to the south-east (Deacon et al. 1992). In the Cape Peninsula particularly, high environmental heterogeneity, was found to be the best predictor of plant species richness (Simmons & Cowling 1996). Here, the highest beta diversity was recorded along soil fertility gradients (Simmons & Cowling 1996). This extremely rich biome begs the question of what the animal diversity must be compared to the plant diversity. Patterns of species richness and the mechanisms driving these have been well investigated in the CFR for groups such as birds (Greve at al. 2011), mammals (Andrews & O’Brien 2000), reptiles (Tolley & Burger 2007) and amphibians (Mokhatla et al. 2012). In contrast, invertebrate richness has not been comprehensively investigated.

It was first noted by Marloth (1908) that “*local botanists as well as entomologists have repeatedly noticed that often there seems to be an entire absence of insect life, although the* *fields or the hillsides may be aglow with flowers*". Johnson (1992) added by saying "*anyone expecting to find fynbos teeming with insect life is bound to be disappointed*". Whilst early arguments suggested that the high plant diversity is not reflected in the arthropod diversity and that insect species richness is low compared to other comparable areas (Johnson 1992, Giliomee 2003), these observations might have been hampered due to the large number of invertebrates and a shortage of taxonomic expertise (Picker & Samways 1996). New evidence suggests that the situation is considerably more complex than was previously thought (Wright & Samways 1998, Procheş & Cowling 2006, Procheş et al. 2009).

Recent studies have found the CFR to be the hotspot of endemism for insect species such as dragonflies (Picker & Samways 1996), gall-insects (Wright & Samways 1998) and bees (Kuhlmann 2009). High local diversity has been found for endophagous insects in the fynbos (Wright & Samways 2000). Also, Wright & Samways (1998) found that gall-insect species richness was positively correlated with the CFR plant species richness. Using more groups of insects, this relationship has also been found by Procheş & Cowling (2006) and Procheş et al. (2009). Indeed, Procheş & Cowling (2006) found that fynbos insect diversity was not as poor as previously thought, although insect diversification did not match plant diversification entirely. In congruence with global norms, these authors found that the variation in insect species richness explained by plant species richness increased with spatial scale. Similarly, high regional richness was also found for monkey beetles in the Succulent Karoo (Colville et al. 2002). Host specificity, a highly heterogeneous habitat and elevation could explain the trends in plant-insect diversity relationship in the CFR (Procheş et al. 2009, Pryke & Samways 2008, 2009). A recent study by Braschler et al. (2012) showed that the local ant species richness in the Fynbos and Succulent Karoo were similar to comparable habitats in other regions of the world.

That the CFR has a high number of endemic insect species is also of importance. On the Cape Peninsula, Picker & Samways (1996) found a significant correlation between the distribution of endemics plant and endemic invertebrate species, and recorded a total of 111 endemic invertebrate species from the literature. They found that areas such as streams, caves and riverine forests had the highest number of endemics. This may be possibly related to historical isolation and topography. Sandstone caves in the Cape Peninsula have been found to be particularly rich in endemic insects, with 21 species, of which many may be regarded as

Endangered (Sharratt et al. 2000). In the same area, more than 90% of the ant species are endemic to South Africa (Robertson 2000). The documentation of these rare endemics is vital for prioritising conservation areas, as fires, invasive species, or urbanisation may lead to the extinction of a species (Rouget et al. 2003).

Although much work on insect species richness patterns has been done in South Africa (Davis 1997, McGeoch & Chown 1997, Hull et al. 1998, van Jaarsveld et al. 1998, Davis et al. 1999, Koch et al. 2000, Davis et al. 2004, Procheş & Cowling 2006, Procheş et al. 2009), little is understood about the relationships between components of diversity for terrestrial insects in the fynbos, such as what the relative contributions are of alpha and beta diversity to total regional diversity (but see Braschler et al. 2012, Pryke & Samways 2012). Thus, although there is evidence that the CFR has a high richness of invertebrates, little is known for soil fauna.

Landscape Influences

Habitat destruction (overexploitation), pollution, invasive species and climate change are recognised as the five major drivers of environmental change (Millennium Ecosystem Assessment 2005). It is important to understand the impact of these drivers and their interactions on biodiversity to be able to make conservation decisions based on more accurate information.

Not only do the drivers of biodiversity gradients in the fynbos remain poorly investigated in terms of their impacts, but the effects of landscape transformation have also not been explored for a wide range of taxa. This is particularly important given the extent of human influence over the landscape globally and in the fynbos biome (Rouget et al. 2003). It has been suggested that 30% of the CFR has been transformed as a result of urbanisation (1.6%), agriculture (25.9%) and by alien trees (1.6%) (Rouget et al. 2003). These figures are expected to increase in the future, and the loss of habitat could ultimately lead to the loss of species (Rouget et al. 2003). Biological invasions, such as by the Argentine ant (*Linepithema humile*), have also been shown to displace some indigenous taxa (Donnely & Giliomee 1985, Lach 2008), although the full extent of this is not yet known.

Together with the anthropogenic influences mentioned above, fire is the main form of disturbance in the fynbos and varies with intensity, occurrence and frequency, which in turn influences plant diversity (Bond & van Wilgen 1996, Thuiller et al. 2007). Fire is thought to be the main process for the mineralisation of slowly decomposing litter in the fynbos, although other decomposition processes are also important between fires (Stock & Lewis 1986, van Wilgen & le Maitre 1986). There has been an increase in fire frequency due to climate change, invasive species and anthropogenic ignition, resulting in fires that need to be increasingly managed in reserves to protect properties (and humans) from damage (van Wilgen 2009, van Wilgen et al. 2011). Thus, it is important to know how the diversity and abundance of species will be influenced by fire effects, especially the ‘unnatural’ high frequency of the fires.

Due to the importance of fire in the fynbos biome, a large number of studies has investigated the effect of fire on indigenous and invasive plants and soil chemical properties (Brown & Mitchell 1986, van Reenen et al. 1992, van Wilgen et al. 1992, Bond & van Wilgen 1996). Fire intensity has been shown to significantly alter soil chemical properties and microbial activity in the fynbos (Brown & Mitchell 1986, van Reenen et al. 1992, Cilliers et al. 2005). Research on the response of invertebrates to fire in the fynbos has mainly been on grasshoppers (Chambers & Samways 1998) and ants (Donnelly & Giliomee 1985, de Kock et al. 1992). Yet, only a few studies have determined the effect of fire on fauna in South Africa, especially on invertebrates (Parr & Chown 2003). In the fynbos, only a few studies have been undertaken on the effects of fire on the abundance and species richness of invertebrates, mainly on ants (Donnelly & Giliomee 1985, de Kock et al. 1992, Pryke & Samways 2012). This is surprising considering the immense importance placed on fire in this biome (Bond & van Wilgen 1996). It has been shown elsewhere that fire may play a significant role in the diversity of soil organisms such as Collembola (Malmström et al. 2009), data is lacking for such groups in South Africa.

As some species of Collembola can survive fires by occurring deeper in the soil, they have been found to be some of the earliest post-fire colonisers (Brand 2002). For Collembola, responses to fire of species can vary considerably, and can mainly be attributed to fire intensity (Brand 2002, Malmström et al. 2009). Here, refugia such as stones, deeper soils and moist litter layers, may play a vital role in the re-colonisation of species. Yet, specialised and restricted species may be eliminated by more intense fires (Brand 2002). Nonetheless, species richness and abundances decrease significantly after a fire, and take considerable time to recover, especially surface-dwelling species (Malmström et al. 2009). Furthermore, the severity of a fire (depth) can influence the recovery of a species after a fire (Malmström et al. 2008). Recovery can also be influenced by factors such as a change in vegetation structure, temperature changes, soil properties such as pH, and difference in food resources such as fungal biomass (Malmström et al. 2009). In contrast to a decrease in abundance as has been found elsewhere, Collembola diversity has been found to actually increase after a fire in Australia using pitfall traps (Greenslade & Rosser 1984). Nonetheless, although pitfall traps are frequently used for after-fire research as most litter is burnt, pitfall traps may give an indication of activity rather of population size (Whelan 1995).

This Thesis

The main aim of the research reported in this thesis is to document the ecological, morphological and molecular diversity of Collembola and the possible correlates thereof in the Fynbos biome. To assess the taxonomic and molecular diversity of Collembola, a combination of published records, sampling and DNA barcoding techniques are used. An historical overview of the number of species described and recorded from South Africa is provided as an appendix. In addition to synthesizing all primary and secondary literature, an updated species list is developed from sampling efforts from 2008-2012 (Chapter 2). The first step was to increase current taxonomic knowledge of Collembola in general. This was achieved by sampling Collembola as broadly as possible in the Western Cape using various techniques. From the collections new species were discovered and species descriptions were undertaken, as illustrated in Chapters 3, 4 and 5. In addition to starting work on the systematics of Collembola, their local and regional diversity was investigated in two ways. First, to investigate the effect of disturbance on a local scale, the effect of fire on Collembola diversity was explored in Jonkershoek Nature Reserve using litterbags (Chapter 6). Specifically, the question whether Collembola are resilient to fire was addressed. Second, on a larger scale using a similar sampling technique, the relationship between alpha and beta diversity was investigated (Chapter 7). Here the role of species richness vs. species turnover in explaining the species richness patterns observed is tested. Based on this research several proposals for future work are made (Chapter 8).

References

Andrews, P. & O'Brien, E.M. (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology* **251**, 205-231.

Bardgett, R.D. & Wardle, D.A. (2010) *Above-below ground linkages. Biotic Interactions, Ecosystems Processes, and Global Change.* Oxford University Press, Oxford.

Blakith, R.E. (1974) The ecology of Collembola in Irish blanket bogs. *Proceedings of R.I.A.* **74**, 2023-226.

Bond, W.J. & van Wilgen, B.W. (1996) *Fire and Plants*. Chapman & Hall, London.

Botes, A., McGeoch, M.A. & Chown, S.L. (2007) Ground-dwelling beetle assemblages in the northern Cape Floristic Region: patterns, correlates and implications. *Austral Ecology* **32**, 210-224.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P. & Chown, S.L. (2006) Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**, 71-90.

Brand, R.H. (2002) The effect of prescribed burning on epigeic springtails (Insecta: Collembola) of woodland litter. *American Midland Naturalist* **148**, 383-393.

Braschler, B., Gaston, K.J. & Chown, S.L. (2012) The Fynbos and Succulent Karoo biomes do not have exceptional local ant richness. *PloSONE* **7**, e31463.

Brown, G. & Mitchell, D.T. (1986) Influence of fire on the soil phosphorus status in sand plain lowland fynbos, south-western Cape. *Suid Afrikaanse Tydskrif van Plantkunde* **52**, 67-72.

Caruso, T., Hogg, I.D., Carapelli, A., Frati, F. & Bargagli, R. (2009) Large-scale spatial patterns in the distribution of Collembola (Hexapoda) species in the Antarctic terrestrial ecosystems. *Journal of Biogeography* **36**, 879-886.

Cassagne, N., Gauquelin, T., Bal-Serin, M-C. & Gers, C. (2006) Endemic Collembola, privileged bioindicators of forest management. *Pedobiology* **50**, 127-134.

Chambers, B. Q. & Samways, M. J. (1998) Grasshopper response to a 40 year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodiversity and Conservation* **7**, 985–1012.

Chown, S.L., van Rensburg, B.J., Gaston K.J., Rodrigues, A.S.L. & van Jaarsveld A.S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* **13,** 1233–1241.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2661-2667.

Cilliers, C.D., Esler, K.J. & Boucher, C. (2005) Effects of alien plant management, fire and soil chemistry on selected soil microbial populations in the Table Mountain National Park, South Africa. *South African Journal of Botany* **71**, 211-220.

Coates, T.J. (1968a) The Collembola from South Africa – I: The Genus *Neanura*. *Journal of the Entomological Society of southern Africa* **31**, 185-195.

Coates, T. J. (1968b). The Collembola of South Africa – 2: The Genus *Seira*. *Journal of the Entomological Society of southern Africa* **31**, 435-462.

Collins, N.J., Baker, J.H. & Tilbrook, P.J. (1975) Signy Island, Maritime Antarctic. In: T. Rosswell & O.W. Heal (Eds.), Structure and function of tundra ecosystems. *Ecological Bulletin* (Sweden) **20**, 345-374.

Colville, J. Picker, M.D. & Cowling R.M. (2002) Species turnover of monkey beetles (Scarabaeidae: Hopliini) along environmental and disturbance gradients in the Namaqualand region of the succulent Karoo, South Africa. *Biodiversity & Conservation* **11**, 243-264.

Coulson, S., Leinaas, H.P., Ims, R.A. & Søvik, G. (2000) Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. *Ecography* **23**, 299-306.

Cowling, R.M., Holmes, P.M. & Rebelo, A.G. (1992) Plant diversity and endemism. In: *The Ecology of Fynbos: Nutrients, Fire and Diversity* (ed. by R.M. Cowling). Oxford University Press, Cape Town, pp. 62-112.

Cowling, R.M., MacDonald, I.A.W. & Simmons, M.T. (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation* **5**, 527-550.

Currie, D. (1991) Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* **137**, 27-49.

Currie, D. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature* **329**, 326-327.

Davies, G., Orme, C. D.L., Storch, D., et al. (2007) Topography, energy and the global distribution of bird species richness. *Proceedings of The Royal Society B* **274**, 1189-1197

Davis A.L.V. (1997) Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae *s. str.*). *African Journal of Ecology* **35**, 10-38.

Davis A.L.V., Scholtz C.H. & Chown S.L. (1999) Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* **26**, 1039-1055.

Davis A.L.V., Scholtz C.H., Dooley P.W., Bharm N. & Kryger U. (2004) Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *South African Journal of Science*, **100** 415-424.

Deacon, H.J., Jury, M.R. & Ellis, F. (1992) Selective regime and time. In: *The Ecology of Fynbos: Nutrients, Fire and Diversity*. R. M. Cowling (Ed.), pp. 6–22. Oxford University Press, Cape Town.

Decaëns, T. (2010) Macroecological communities in soil communities. *Global Ecology and Biogeography* **19**, 287-302.

Deharveng, L. (1996) Soil Collembola diversity, endemism, and reforestation: a case study in the Pyrenees (France). *Conservation Biology* **10**, 74-84.

de Kock, A.E., Giliomee, J.H., Pringle, K.L. & Majer, J.D. (1992) The influence of fire, vegetation age and Argentine ants (*Iridomyrmyx humilis*) on ant communities on Swartboskloof. In: *Fire in South African Mountain Fynbos. Ecosystem, Community and Species Response at Swartboskloof*. B.W. van Wilgen, D.M. Richardson, D.M., Kruger, F.J. & van Hensbergen (Eds), pp. 203-215. Springer-Verlag, Berlin.

Donnelly D. & Giliomee J. H. (1985) Community structure of epigaeic ants in a pine plantation and in newly burnt fynbos. *Journal of the Entomological Society of South Africa* **48**, 259–65..

Dupont, L.M., Linder, H.P., Rommerskirchen, F. & Enno Schefuß, E. (2011) Climate-driven rampant speciation of the Cape flora. *Journal of Biogeography* **38**, 1059–1068.

Ermilov, S.G. & Hugo-Coetzee, E.A. (2012) The oribatid mite genus *Nothrus* Koch, 1836 (Acari: Oribatida: Nothridae) of South Africa, including a key to African species. *Zootaxa* **3243**, 29-51.

Ettema, C.H. & Wardle, D.A. (2002) Spatial soil ecology. *Trends in Ecology and Evolution* **17**, 177-183.

Evans K.L., van Rensburg B.J., Gaston K.J. & Chown S.L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography* **15**, 625-636.

Francis, A.P. & Currie, D.J. (1998) Global patterns of tree species richness in moist forest: another look. *Oikos* **81**, 598–602.

Gabriel A.G.A., Chown S.L., Barendse J., Marshall D.J., Mercer R.D., Pugh P.J.A. & Smith V.R. (2001) Biological invasions on Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Gaertner, M., Den Breeyen, A., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography* **33**, 319-339.

Gaston K.J., Davies R.G., Orme C.D.L., Olson V.A., Thomas G.H., Ding T.-S., Rasmussen P.C., Lennon J.J., Bennett P.M., Owens I.P.F. & Blackburn T.M. (2007) Spatial turnover in the global avifauna. Proceedings of the Royal Society of London B **274**, 1567-1574.

Giliomee, J.H. (2003) Insect diversity in the Cape Floristic Region. *African Journal of Ecology* **41**, 237-244.

Goldblatt, P. (1978) An analysis of the flora of Southern Africa: its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden* **65**, 369-436.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape region of Southern Africa. *Annals of the Missouri Botanical Garden* **89**, 281–302.

Gonzalez-Voyer, A., Padial, J. M., Castroviejo-Fisher, S., et al. (2011) Correlates of species richness in the largest Neotropical amphibian radiation. *Journal of Evolutionary Biology* **24**, 931-942.

Greenslade, P. & Rosser, G. (1984) Fire and soil-surface insects in the Mount Lofty Ranges, South Australia. In *Medecos IV*. Dell, B. (Ed), pp.63-64. University of Western Australia.

Greve, M., Chown, S.L., van Rensburg, B.J., Dallimer, M. & Gaston, K.J. (2011) The ecological effectiveness of protected areas: a case study for South African birds. *Animal Conservation* **14**, 195-305.

Helme, N.A. & Trinder-Smith, T.H. (2006) The endemic flora of the Cape Peninsula, South Africa. *South African Journal of Botany* **72**, 205-210.

Heywood, V.H. (1995) *Global Biodiversity Assessment*. Cambridge University Press, Cambridge.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist* **163**, 192-211.

Hopkin, S. (1997) *Biology of the Springtails. Insecta: Collembola*. Oxford University Press, Oxford.

Hull H.E., Freitag S., Chown S.L. & Bellamy, C.L. (1998) Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. *African Entomology* **6**, 265-274.

Huntley, B.J. (1989) *Biotic Diversity in Southern Africa: Concepts and Conservation*. Oxford University Press, Cape Town.

Jetz, W. & Fine, P.V.A. (2012) Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLOS BIOLOGY* **10**, e1001292.

Johnson, S.D. (1992) Plant–animal relationships. In: *The Ecology of Fynbos: Nutrients, Fire and Diversity*. R.M. Cowling (Ed.), pp. 175–205. Oxford University Press, Cape Town.

Kaneko, N. & Salamanca, E.F. (1999) Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecological Research* **14**, 231-138.

Kennedy, A. (1994) Simulated climate change: a field manipulation study of polar microarthropod community response to global warming. *Ecography* **17**, 131-140.

Koch S.O., Chown S.L., Davis A.L.V., Endrödy-Younga S. & Van Jaarsveld A.S. (2000) Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. *Journal of Insect Conservation* **4,** 45-56.

Kuhlmann, M. (2009) Patterns of diversity, endemism and distribution of bees (Insecta: Hymenoptera: Anthophila) in Southern Africa. *South African Journal of Botany* **75**, 726-738.

Lach, L. (2008) Argentine ants displace floral arthropods in a biodiversity hotspot. *Diversity and Distribution* **14**, 281-290.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. & Rossi, J.P. (2006) Soil invertebrates and ecosystem services. *European Journal of Soil Biology* **42**, S3-S15.

Lawrence, R.F. (1953) *The biology of the cryptic fauna of forests. With special reference to the indigenous forest of South Africa.* Balkema: Cape Town.

Linder, H.P. (1991) Environmental correlates of patterns of species richness in the south-western Cape Province of South Africa. *Journal of Biogeography* **18**, 509-518.

Linder, H.P. (2003) The radiation of the Cape flora, southern Africa. *Biological Reviews* **78**, 597-638.

Malmström, A., Persson, T. & Ahlström, K. (2008) Effects of fire intensity on survival and recovery of soil microarthropods after a clearcut burning. *Canadian Journal of Forestry Research* **38**, 2465-2475.

Malmström, A., Persson, T., Ahlström, K., Gongalsky, K.B. & Bengtsson, J. (2009) Dynamics of soil meso- and macrofauna during a 5-year period after clear-cut burning in a boreal forest. *Applied Soil Biology* **43**, 61-74.

Marloth, R. (1908) Some observations on entomophilous flowers. *South African Journal of Science* **4**, 110-113.

McGeoch, M.A. & Chown, S.L. (1997) Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: the importance of reserves in urban areas. *Biodiversity and Conservation* **6**, 979-993.

Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powrie L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology & Biogeography* **11**, 445-451.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis.* World Resources Institute, Washington, DC.

Mittermeier, R.A., Robles-Gil, P., Hoffmann, M., Pilgrim, J.D., Brooks, T.M., Mittermeier, C.G., Lamoreux, J.L. & Fonseca, G. (2004) *Hotspots Revisited: Earth's Biologically Richest and Most Threatened Terrestrial Ecoregions*. Cemex & Conservation International, Mexico City.

Mokhatla, M.M., Measey, G.J., Chimimba, C.T. & van Rensburg, B.J. (2012) A biogeographical assessment of anthropogenic threats to areas where different frog breeding groups occur in South Africa: implications for anuran conservation. *Diversity and Distributions* **18**, 470-480.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 583-858.

Nardi, F., Spinsanti, G., Boore, J.L., Carapelli, A., Dallai, R. & Frati, F. (2003) Hexapod origin: monophyletic or paraphyletic? *Science* **299**, 1887-1889.

Parr, C.L. & Chown, S.L. (2003) A burning issue for conservation: A critique of faunal fire research in Southern Africa. *Austral Ecology* **28**, 384-395.

Parr, C.L., Robertson, H.G., Biggs, H.C. & Chown, S.L. (2004) Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* **41**, 630-642.

Parr, C.L., Robertson, H.G. & Chown, S.L. (2003) Apomyrminae and Aenictogitoninae: two new subfamilies of ant (Hymenoptera: Formicidae) for southern Africa. *African Entomology* **11**, 128-129.

Parr, C.L., Sinclair, B.J., Andersen, A.A., Gaston, K.J., & Chown, S.L. (2005) Constraint and competition in assemblages: a cross- continental and modeling approach for ants. *American Naturalist* **65**, 481-494.

Petersen, H. & Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* **39**, 287-388.

Picker, M.D & Samways, M.J. (1996) Faunal diversity and endemicity of the Cape Peninsula, South Africa- a first assessment. *Biodiversity and Conservation* **5**, 591-606.

Plisko, J. D. (2010) Megadrile earthworm taxa introduced to South African soils (Oligochaeta: Acanthodrilidae, Eudrilidae, Glossoscolecidae, Lumbricidae, Megascolecidae, Ocnerodrilidae). *African Invertebrates* **51**, 289-312.

Procheş, S. & Cowling, R.M. (2006) Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecology and Biogeography* **15**, 445-451.

Procheş, S., Forest, F., Veldtman, R, Chown, S.L., Cowling, R.M., Johnson, S.D., Richardson, D.M. & Savolainen, V. (2009) Dissecting the plant-insect diversity relationship in the Cape. *Molecular Phylogenetics and Evolution* **51**, 94-99.

Pryke, J.S. & Samways, M.J. (2008) Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation* **17**, 3027-3043.

Pryke, J.S. & Samways, M.J. (2009) Conservation of the insect assemblages of the Cape Peninsula biodiversity hotspot. *Journal of Insect Conservation* **13**, 627-641.

Pryke, J.S. & Samways, M.J. (2012) Importance of using many taxa and having adequate controls for monitoring impacts of fire for arthropod conservation. *Journal of Insect Conservation* **16**, 177-185.

Raschmanová, N., Kováč, L. & Miklisová, D. (2008) The effects of mesoclimate on Collembola diversity in the Zádiel Valley, Slovak Karst (Slovakia). *European Journal of Soil Biology* **44**, 463-472.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L. & Rutherford, M.C. (2006) Fynbos Biome. In: *The Vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia* 19, pp. 52-219. L. Mucina & M.C. Rutherford (eds.) South African National Biodiversity Institute, Pretoria.

Richardson D.M., Rouget M., Ralston S.J., Cowling R.M., van Rensburg B.J. & Thuiller W. (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience* **12**, 391-402.

Robson, T.C., Baker, A.C. & Murrray, B.R. (2009) Differences in leaf-litter invertebrate assemblages between *radiata* pine plantations and neighbouring native eucalypt woodland. *Austral Ecology* **34**, 368-376.

Roets, F., de Beer ZW, Dreyer LL, Zipfel R, Crous PW, Wingfield MJ. (2006) Multigene phylogeny for *Ophiostoma* spp. reveals two new species from *Protea* infructescences. *Studies in Mycology* **55**, 199–212.

Robertson, H.G. (2000) Afrotropical ants (Hymenoptera: Formicidae): taxonomic progress and estimation of species richness. *Journal of Hymenoptera Research* **9**, 71-84.

Robertson, H.G. (2002) Revision of the ant genus *Streblognathus* (Hymenoptera: Formicidae: Ponerinae). *Zootaxa* **97**, 1-16.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current pattern of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* **112**, 63–85.

Rusek, J. (1985) Soil microstructures-contributions on specific soil organisms. *Quaestiones Entomologicae* **21**, 497-514.

Rusek, J. (1998) Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation* **7**, 1207-1219.

Safi, K. Cianciaruso, M.V., Loyola, R.D., et al. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B* **366**, 2536-2544.

Salamon, J.-A. & Alphei, J. (2009) The Collembola of a Central European forest: influence of tree species composition. *European Journal of Soil Biology* **45**, 199-206.

Salamon, J.-A., Schaefer, M., Alphei, J., Schmid, B. & Scheu, S. (2004) Effects of plant diversity on Collembola in an experimental grassland ecosystem. *Oikos* **106**, 51-60.

Sharratt, N.J., Picker, M.D. & Samways, M.J. (2000) The invertebrate fauna of the sandstone caves of the Cape Peninsula (South Africa): patterns of endemism and conservation priorities. *Biodiversity and Conservation* **9**, 107-143.

Simmons, M.T. & Cowling, R.M. (1996) Why is the Cape Peninsula so rich in plant species? An analysis of the independent diversity components. *Biodiversity and Conservation* **5**, 551-573.

Sinclair, B.J. & Stevens, M.I. (2006) Terrestrial microarthropods of Victoria Land and Queen Maud Mountains, Antarctica: implications of climate change. *Soil Biology & Biochemistry* **38**, 3158-3170.

Slabber, S., Worland, M.R., Leinaas, H.P. & Chown, S.L. (2007) Acclimation effects on thermal tolerances of springtails from sub-Antarctic Marion Island: Indigenous and invasive species. *Journal of Insect Physiology* **53**, 113-125.

Sousa, J.P., Bolger, T., da Gama, M.M., Lukkari, et al. (2006) Changes in Collembola richness and diversity along a gradient of land-use intensity: A pan European study. *Pedobiologia* **50**, 147-156.

Stock, W.D. & Lewis, O.A.M. (1986) Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *Journal of Ecology* **74**, 317-328.

Thomas G.H., Orme C.D.L., Davies R.G., Olson V.A., Bennett P.M., Gaston K.J., Owens I.P.F. & Blackburn T.M. (2008) Regional variation in the historical components of global avian species richness. *Global Ecology and Biogeography* **17**, 340-351.

Thuiller W., Midgley G.F., Rouget M. & Cowling R.M. (2006) Predicting patterns of plant species richness in megadiverse South Africa. *Ecography* **29**, 733-744.

Thuiller, W., Slingsby, J.A., Privett, S.D.J. & Cowling, R.M. (2007) Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. *PLoS ONE* **9**, e938.

Tolley, K.A. & Burger, M. (2007) *Chameleons of Southern Africa*. Struik.

Ulrich, W. & Fiera, C. (2009) Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologia* **35**, 45-52.

Ulrich, W. & Fiera, C. (2010) Environmental correlates of body size distributions of European springtails (Hexapoda: Collembola). *Global Ecology & Biogeography* **19**, 905-915.

Vanbergen, A.J., Watt, A.D., Mitchell, R., Truscott, A.-M., Palmer, S.C.F., Ivits, E., Eggleton, P., Jones, T.H. & Sousa, J.P. (2007) Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. *Oecologia* **153**, 713-725.

van Jaarsveld A.S., Freitag S., Chown S.L., Muller C., Koch S., Hull H., Bellamy C., Krüger M., Endrödy-Younga S., Mansell M.W. & Scholtz C.H. (1998) Biodiversity assessment and conservation strategies. *Science* **279**, 2106-2108.

van Reenen, C.A., Visser, G.J. & Loos, M.A. (1992) Soil microorganisms and activities in relation to season, soil factors and fire. In: *Fire in South African Mountain Fynbos. Ecosystem, Community and Species Response at Swartboskloof*. B.W. van Wilgen, D.M. Richardson, D.M., Kruger, F.J. & van Hensbergen (Eds.), pp. 240-257. Springer-Verlag, Berlin.

van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist* **159**, 566-577.

van Straalen, N.M. (1994) Adaptive significance of temperature responses in Collembola. *Acta Zoologica Fennica* **195**, 135-142.

van Wilgen, B.W. (2009) The evolution of fire and invasive alien plant management practices in fynbos. *South African Journal of Science* **105**, 335-342.

van Wilgen, B.W., Govender, N, Forsyth, G.G. & Kraaij, T. (2011) Towards adaptive fire management for biodiversity conservation: Experience in South African National parks. *Koedoe* **53**, art # 982, 9 pages.

van Wilgen, B.W. & le Maitre, D.C. (1986) Preliminary estimates of nutrient levels in the fynbos vegetation and the role of fire in nutrient recycling. *South African Forestry Journal* **119**, 24-28.

van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & van Hensbergen (Eds) (1992) *Fire in South African Mountain Fynbos. Ecosystem, Community and Species Response in Swartboskloof.* Springer Verlag, Berlin.

Wallwork, J.A. (1972) Distribution patterns and population dynamics of the micro-arthropods if a desert soil in Southern California. *Journal of Animal Ecology* **41**, 291-310.

Wardle, D.A. (2002) *Communities and ecosystems: linking the aboveground and belowground components*. Princeton University Press, New Jersey.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629-1633.

Whelan, R.J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**, 379-338.

Wilson, J. B., Peet, R. K., Dengler, J., et al. (2012) Plant species richness: the world records. *Journal of Vegetation Science* **23**, 796-802.

Wright, M. & Samways, M.J. (1998) Insect species richness tracking plant species richness in a diverse flora: gall insects in the Cape Floristic Region, South Africa. *Oecologia* **115**, 427-433.

Wright, M.G. & Samways, M.J. (2000) Biogeography and species richness of endophagous insects associated with Proteaceae in South Africa. *African Journal of Ecology* **38**, 16-22.

Chapter 2

Collembola of South Africa:

Current knowledge and
Future perspectives

Introduction

The documentation of baseline biodiversity information is essential for the conservation of species worldwide. Biodiversity assessments and monitoring programmes often use arthropods as surrogates to determine the diversity of an area, and several well established methods exist (Samways et al. 2010). However, while the interest in biodiversity has increased in various fields, the number of trained taxonomists has decreased (Kim 1993, Jinbo et al. 2011). The taxonomic impediment and its implications for biodiversity studies have been widely discussed (Godfray 2002, Samper 2004). Despite these challenges, globally taxonomic knowledge is increasing for popular groups such as arachnids, beetles and ants (Nillsson-Örtman & Nilsson 2010, AntWeb V4.110 www.antweb.org, The World Spider Catalogue V13.0 http://research.amnh.org/iz/spiders/catalog). This is also true for South Africa (Foord et al. 2002, Robertson 2000, 2002, Parr et al. 2003, Haddad & Dippenaar-Schoeman 2006, Dippenaar-Schoeman & González Reyes 2006, Dippenaar-Schoeman et al. 2006, Hlavac 2007). However, as in many other under-sampled countries, the soil fauna has not been well investigated, and soil diversity remains very poorly known despite its importance shown elsewhere (Wardle et al. 2004).

Collembola are amongst the most widespread and abundant soil arthropods (Petersen & Luxton 1982, Hopkin 1997). Although 8200 species of Collembola are known to exist (Bellinger et al. 2012), this is thought to represent only 10% of the estimated number of species (Deharveng 2004). This is not only due to a lack of taxonomic expertise (as found in many other taxa), but also to the lack of records or sampling from all continents (Rusek 1998). However, over the past few decades, considerable progress has been made in Collembola taxonomy (Deharveng 2004). These include the development of new stable morphological characters for species descriptions, including antennal, leg and dorsal chaetotaxy.

A promising way to overcome the taxonomic impediment is through DNA barcoding, an approach based on the unique genetic profile that characterizes distinct species. DNA barcoding is especially useful when applied to poorly known groups, where a rapid assessment of the molecular diversity can be done before the conventional taxonomic work (Hajibabaei et al. 2006). A DNA barcoding approach to distinguish closely related species has been used for several invertebrate groups (Hebert et al. 2003) and has also been successfully applied to Collembola in this respect (Hogg & Hebert 2004, Porco et al. 2010a). Barcoding has been successfully used for the re-description of species (Stevens et al. 2006), and has proved to be a useful complement to traditional morphological taxonomy for biodiversity inventories (Hogg & Hebert 2004). It is especially important for species showing colour variations or for identifying juvenile specimens, as many species undergo morphological changes during successive instars. In these cases the misidentification of a specimen is highly likely, thus the use of barcoding can prevent these mistakes as a DNA profile is consistent across all life stages. Through these advances, Collembola are being increasingly used as model organisms in ecological and large scale studies (e.g. Urlich & Fiera 2009, 2010, Fiera & Ulrich 2012). However, our knowledge of South African Collembola is too poor to allow such macroecological approaches.

The first attempt to collate all taxonomic information on the Collembola South Africa was undertaken in the form of an unpublished species list by P. Greenslade, (http://www.ru.ac.za/static/departments/zoo/Martin/acollembola.html). To date there are an estimated 30 publications for Collembola recorded or described from South Africa; the earliest from Börner (1908). Most notably, comprehensive descriptions were made by Paclt (1959, 1964, 1965, 1967), Coates (1968a, 1968b, 1969) and later Barra (1994, 1995, 1997, 1999, 2001, 2002, Barra & Weiner 2009). In addition, Lawrence (1953) sampled in forests, and drew attention to the diversity and functional importance of litter and soil fauna in South Africa. Since 2008 a large project has sampled the Cape Floristic Region extensively under the bilateral South Africa–France Protea I and Protea II projects, with the aim to investigate the taxonomic and genetic diversity of Collembola in the Fynbos Biome (Janion et al. 2011a). The aim of this paper is to present all collated information of Collembola recorded from South Africa in the literature and from the recent sampling, to provide an updated species list for the Western Cape using DNA barcoding as a tool to aid in species identification.

Methods

Literature

All publications of Collembola species described or recorded from South Africa were collected using Web of Science and Google Scholar. In addition, an unpublished species list entitled “The Aquatic Springtails (Insecta: Collembola) of South Africa” by Penelope Greenslade was available on a website (Greenslade, unknown year). Nomenclature follows Bellinger et al. (2012), as the nomenclature of certain taxonomic groups may have changed since the original description of the species. The following information was obtained (where available): collection details including date, collector, place, town, habitat type, and collection method, type locality and accession number if given by the author or museum. A species was considered dubious as a result of misidentification, or because its given species name does not match a clearly recognized species. This was done in consultation with Dr. Deharveng who is an expert in this field of Collembola taxonomy and distribution. Nevertheless, every record from the literature was included (Table 1 Supplementary Material), even sub-species. However, all species found dubious or recorded as subspecies were not included in the updated species list for South Africa (Table 1). The species were assigned a South African province from the locality recorded. The species were also divided into endemic if they were described from South Africa and have not been recorded elsewhere, introduced, if the species was described from another continent and considered an introduced species or has a cosmopolitan distribution, or pantropical, when the species is known to occur in tropical regions. When available, notes on the origin of the introduced species are made in the ‘Comments’ column of Table 1.

Sampling

Samples used to compile the current species list were collected by various individuals over the period 2008-2012. They include 366 litter samples (one litre) and 530 litterbags samples (height = 4 cm, diameter = 7.5 cm, bottom mesh size 0.5 mm, top mesh size 1.6 mm, see Chapter 6 and 7 for more details, collected by C. Janion), 427 litter and soil samples (0.5 – 1 litre, collected by L. Deharveng and A. Bedos leg), and 80 litter samples (one litre, collected by A. Liu leg, Liu et al. 2012). The litterbag study which was done in a more systematic fashion than the litter or soil sampling, where at least 40 traps were deployed per site. Various sampling techniques were used in as many localities and different microhabitats as possible throughout the Western Cape, including Afromontane forest, different fynbos vegetation types, intertidal habitats, caves and disturbed areas such as gardens and agricultural areas. Figure 1 shows all the sampling points to date. Leaf litter, moss, rotten wood and soil samples (500 ml or 1 litre) were taken at different sampling sites over the duration of the project (2008-2012). Sampling sites were usually in nature reserves where about 20 samples were taken, although opportunistic sampling was also done, where only a couple of samples were taken for barcoding purposes. It has been shown that about 10 samples are sufficient to capture the species richness in an area (Liu et al. 2012). Disturbed areas such as farm dams, irrigated gardens or exotic tree plantations were sampled to collect potentially introduced species. All samples were extracted by means of a Tullgren-Berlese extraction for five to seven days, or until dry (Berlese 1905, Tullgren 1918). In addition, active searching was done in the field; soil was sieved next to rivers to collect water-dependent species, which were collected with a fine brush. Fine sand such as sea sand was washed in the laboratory and animals were also collected with a brush. Vegetation such as branches from bushes, fynbos shrubs, and grasses was beaten over a tray and animals were collected by means of an aspirator. Finally, litter bags investigating decomposition rates of fynbos plant species were extracted by means of a high-gradient extractor (Bengtsson et al. 2011, 2012, 40 litterbags per site, also see Chapter 6 and 7). All samples are stored in 96-99% ethanol at the Centre for Invasion Biology (C·I·B), Stellenbosch or the Museum National d'Histoire Naturelle (MNHN), Paris.

Barcoding

Specimens collected through various techniques were barcoded as part of the BCCOL project (Barcoding Collembola project) which aims to barcode the global Collembola fauna. BCCOL is linked to the Barcoding of Life Datasystems (BOLD), which is an online tool "aiding the acquisition, storage, analysis and publication of DNA barcode records" (Ratnasingham & Hebert 2007). Protocols followed those prescribed by BOLD (Ratnasingham & Hebert 2007). For each specimen the following information was provided: species name and identifier (in most cases a morphospecies name was provided for South African specimens), collection information such as date and place of collection including GPS coordinates and collector name, and extra information when necessary such as colour or any descriptive information, especially in our case where the fauna is not well known. Once morphospecies were identified, six individuals were submitted for barcoding, while another two to four were kept in ethanol or mounted on a slide for identification (protocol for Collembola of the World, developed by L. Deharveng). A photograph was taken of each individual using a Leica M125 microscope with a DFC320 digital camera and Leica software. The specimens were placed in a 96-well plate following standard protocols, and sent to the University of Guelph, Ontario, for processing. The gene region targeted is mitochondrial cytochrome oxidase subunit I

(COI), using universal primers as described by Folmer et al. (1994). Once DNA were extracted, the remaining skin (if successfully recovered) is stored in ethanol for reference, as the chaetotaxy characteristics typically used for identification remain preserved after DNA extraction (Porco et al. 2010b). All information was stored and managed online with BOLD (www.boldsystems.org, Ratnasingham & Hebert 2007).

Sequences (consisting of more than 650 basepairs) of the mitochondrial cytochrome oxidase I (COI) haplotypes were aligned manually using BioEdit (Hall 1999). Although a distance-based approach (i.e. a neighbour-joining tree with some correction for different rates of transitions and transversions) is typically adopted under Barcoding, distance-based approaches are over-simplistic in tree-reconstruction as well as in correcting for various evolutionary parameters. As such, an evolutionary more realistic approach was adopted here. Specifically, the model of evolution that best fitted the COI gene for the specimens included here was determined in jModelTest 0.1.1 (Posada 2008) under the Akaike information criterion (AIC) (Akaike 1973). Sequences of *Artemia franciscana* (Branchiopoda: Anostraca: Artemiidae) obtained from GenBank was used as an outgroup. A Bayesian Inference (BI) search approach was used to search tree-space and obtain the best evolutionary topology for the data (MrBayes v. 3.2.1; Ronquist & Huelsenbeck 2003). Monte Carlo Markov Chain (MCMC) simulations were run for 14000000 generations with sampling every 100 generations. The average standard deviation of split frequencies <0.01 is generally accepted as being a relatively good convergence; however, the split frequencies from the run remained above this value. As such, areas of the tree must be interpreted with caution. The majority rule consensus tree was constructed after the first 14000 (or 10%) trees were discarded as burn-in. The posterior probabilities for nodes were calculated by the proportion of time the node was recovered, and values exceeding 0.95 is generally considered as well supported (Holder & Lewis 2003).

From the trees constructed, different lineages could be observed (Figure 2). Different lineages in the same species were assigned different names, for example *Parisotoma* L1, *Parisotoma* L2, etc. These are considered as Molecular Operational Taxonomic Units or MOTUs (see Porco et al. 2012c), thus are species awaiting further morphological investigation.

Results

Updated checklist

Supplementary material Table 1 shows all species recorded from South Africa up to October 2012. This includes 151 species from 63 genera and 17 families. From these, a total of 23 species are considered dubious, while 36 species are thought to be introduced and 92 endemic. The majority of species were described from either the Western Cape or Kwazulu-Natal. For the Western Cape, 72 species have been recorded from 36 genera and 16 families. From these, 45 are endemic while 27 may have been introduced (Table 1).

Many species resembling well-known European species were previously determined accordingly. For example, *Seira squamoornata*, which was originally described from the Ukraine, was thought to be a common polymorphic species in South Africa after Paclt (1959). However, Yosii (1959) did not even include this species in his list, while Coates (1968b) found that specimens labelled as *S. squamoornata* by Paclt (1959) fall into the species described by Yosii (1959) or Coates (1968b), and concluded that this European species does not occur in South Africa. Indeed, to date 25 species of *Seira* have been described from South Africa (Yosii 1959, Coates 1968b). Other examples include several species of *Entomobrya*. For example, *E. nivalis* recorded from South Africa is actually very common in Europe, but all records from the southern hemisphere could be dubious according to Jordana (2012). This species was never found in our samples.

The species *Sminthurus viridis* also known as the Lucerne flea (Wallace 1964, Wallace & Walters 1974) received considerable attention during the late 1960s due to its pest status. It is thought to have arrived from Australia as eggs in soil through the importation of clover seed (Walters 1968, Wallace & Walters 1974). It was first collected in 1941 near Somerset West and by 1959 over 50 000 hectares of Lucerne was infected (Wallace & Walters 1974). The pest status of *S. viridis* in South Africa is currently unknown.

There are currently six endemic genera in South Africa: *Najtafrica* Barra, 2002 (Pseudachorutinae), *Probrachystomellides* Weiner & Najt, 1991 (Brachystomellidae), *Capbrya* Barra, 1999 (Entomobryidae), *Lepidokrugeria* (Lepidocyrtinae) Coates, 1969, *Neophorella* Womersley, 1934 (Tomoceridae) and *Tritosminthurus* Snider, 1988

(Bourletiellidae). *Neophorella dubia* is the only endemic species of the family Tomoceridae to occur in South Africa. However, after our intensive sampling in the Cape Town region (exact type locality of this specimen not given), no example of this species, which was described from a single specimen, has been found.

New species for South Africa

From this project's sampling, 164 species from 76 genera and 21 families have been documented in the Western Cape (Supplementary material, Table 2). The number of species recorded from this region has increased considerably since the start of the project in 2008. Most notable first findings for South Africa include the following: 1) *Mackenziella* cf. *psocoides*, which is the only species of the monotypic family Mackenziellidae, previously only recorded from the Northern Hemisphere (Canary Islands, Canada, Germany, Poland, Norway and Sweden; Fjellberg 2007). This species is often overlooked due its minute size (0.2-0.3 mm). From the current collections, it has only been recorded from one sample in the sand fynbos in Tokai, near Cape Town (Liu et al. 2012); 2) *Isotogastrura* sp. (Isotogastruridae) is also a rare and minute species which has only been found in one locality in South Africa (sea sand in Wilderness). This interesting genus generally occurs in sea sand and shares characters with the families Hypogastruridae and Isotomidae, making its phylogenetic status unclear. It has previously been recorded from only a few locations, including the Canary Islands, New Caledonia, Mexico, Madagascar, Caribbean Islands, and most recently South China (Potapov et al. 2011a); 3) *Triacanthella madiba* (Hypogastruridae) is the first record of the genus *Triacanthella* found in Africa. It was described from a cave near Table Mountain, Cape Town, and it is also the first record of this genus in cave guano (Janion et al. 2012). Since then, other *Triacanthella* specimens have been found in several locations in the Western Cape, and barcoding indicates that at least two species may exist (Supplementary material, Table 3) and 3); 4) *Willowsia* sp. is the first record of the genus Willowsia for Africa, except for the pantropical species *W. jacobsoni* (Zhang et al. 2011).

Species new to science

Certain genera show high diversity, including the isotomids *Parisotoma* (six species with nine MOTUs) and *Cryptopygus* (six species with four MOTUs). Only two species from the *Parisotoma* genus has been recorded from South Africa, *P. mossopi* and *P. notabilis*. However, the presence of *P. notabilis* in South Africa has not been confirmed by the current sampling, and it may thus have been misidentified previously. There is also an indication that at least seven species from the genus *Ectonura* (Neanuridae) exist. Animals from this genus are usually found in damp rotten wood or in some cases in leaf litter and seem to have a wide distribution. From these collections, two new species have been described, namely *Ectonura barrai* and *E. monochaeta* (Janion et al. 2011b). Lastly, the genus *Seira* shows a high diversity, with 25 species described from South Africa (Coates 1968b). From the current sampling, 20 morphospecies were distinguished. The colour pattern was useful as an initial method to identify morphospecies (Figure 3).

Barcoding

To date, a total of 734 specimens from the Western Cape have been successfully barcoded. These consist of 107 Molecular Taxonomic Units (MOTUs) from 35 genera and 12 families (Fig. 2, Supplementary material Table 2, Figure 1). It has been especially useful in cases where there are significant morphological differences in male and females to confirm they belong to the same species (e.g. *Sphaeridia:* Sminthurididae). Barcoding has also been useful to confirm the use of colour pattern for the identification of the genus *Seira*. For this genus alone, 20 morphospecies have been barcoded to date from the Western Cape (Fig. 3). Although many species from this genus have been described by Coates (1969) and Yosii (1959), the taxonomy of this group is not resolved. Although many species were described from the Western Cape, the type localities are not clear, and many species described by these authors were from the Limpopo and Kwazulu-Natal provinces. Thus, to get an indication of the diversity of this group, colour pattern may a useful first measure of a morphospecies, as shown in Figure 3. The species shown in the figure are only from the Western Cape and their collection locality is indicated next to the picture of each species. In addition, another widespread genus, *Parisotoma*, showed a high diversity throughout the Western Cape, also suggesting high endemicity (Fig. 4). For this genus, at least six MOTUs have been recognised for the Western Cape, all from geographically distinct areas. However, two species have been identified from Tokai, where fynbos and pine litter has been sampled. Once more sequences are available from other parts of the world, especially from Europe, the presence of introduced species such as *Parisotoma notabilis* can be confirmed. Of these barcoded, one has already been described, namely *Parisotoma obscurocellata* (Potapov et al. 2011). Surprisingly, the genus *Ceratophysella* has several MOTUs from the current samples (Fig. 5), though it is generally thought to be an introduced genus. From the species barcoded, nine MOTUs were found. With the high molecular diversity found, there is a possibility that South Africa may have endemic species of *Ceratophysella*. However, this is a first assessment of the diversity and may indicate cryptic lineages.

Discussion

The classification and identification of species have been the interest of both taxonomists and ecologists since the beginning of modern classification by Linnæus (1758). While the interest in biodiversity patterns in community structure is increasing, the number of taxonomic experts is decreasing. The use of modern molecular techniques such as DNA barcoding has been proposed as a means to overcome this challenge, although this should be used as a complement to traditional taxonomy (Hogg & Hebert 2004).

From the combination of traditional morphological taxonomy and the existing literature, there are currently 213 Collembola species known from the Western Cape in South Africa from 22 families. However, many of these species need to be verified and confirmed, and the count does not include all MOTUs. From the literature review it appears that many species records are questionable, and for the Western Cape only, almost 30% of the species may have been introduced. Also, it is evident that there is high endemicity in the Collembola fauna, (see e.g. Barra 1999, Coates 1968a, 1968b, 1969, Weiner and Najt 1991; Yosii 1959), and this was confirmed by our results. Endemic species are thought to be more vulnerable to loss of natural habitat than non-endemic species (Deharveng 1996). As they do represent a large proportion of the total assemblages in Western Cape, they could be used to assess the effect of environmental change and habitat disturbance as has been done elsewhere (Cassagne et al. 2006). Among these endemic species, four potential radiations were found, namely in the genera *Seira*, *Parisotoma*, *Cryptopygus* and *Ectonura*. Only one species of the genus *Seira* was thought to occur in South Africa (Womersley 1934, Paclt 1959). The careful taxonomic investigations of Yosii (1959) and Coates (1968b) showed that several characters were stable and useful to characterize South African species, including the macrochaetal formula on thoracic segment II-III, and abdominal segment I Coates (1968b). To date, 24 species of *Seira* have been described from South Africa. Although Coates (1968b) found colour pattern to be an unreliable character in species identification, we have found with barcoding that species of this genus can also be separated by their colour pattern (Figure 2), with 20 lineages found in the Western Cape alone. Further investigations are underway to explore the diversity and distribution of this genus in more detail. For *Cryptopygus*, these preliminary assessments indicate at least six additional species in the Western Cape from the one species previously reported (*C. caecus*). Similarly, *Ectonura* species numbers increased from one to seven (other *Ectonura* species recorded form Kwazulu-Natal), and for *Parisotoma* six additional species are known while two were described from the current samples and one previously recorded is questionable (*P. notabilis* which has not been found to date). The species here could however be more, as this does not include additional MOTUs found through DNA barcoding. However, further taxonomic investigations are needed to confirm these MOTUs as true species.

In addition, with the use of DNA barcoding, 107 MOTUs were found. This indicates a high level of cryptic diversity which is sometimes hard to discover based on taxonomy alone (Deharveng 2004). Barcoding has been useful to confirm several introduced species from Europe to other parts of the world (Porco et al. 2012a, b). Just over 10% of the Collembola taxa in the CFR could have been introduced (Supplementary material, Table 3). This is not entirely surprising as the history of South Africa is intimately linked to that of Europe, specifically France, The Netherlands and the UK (Giliomee & Mbenga 2007). Many of the invasive species were collected in disturbed environments or close to human settlements, such as *Hypogastura manubrialis* which was found to dominate remnant disturbed Renosterveld patches (Leinaas et al. in prep). However, *Ceratophysella* species were present in many natural undisturbed areas, which might be concerning given the effect introduced species can have on native fauna (Terauds et al. 2011). However, several lineages were characterized in the Western Cape *Ceratophysella*, some of which without known counterparts in Europe.

Further studies will have to investigate if these MOTUs can be considered true species. This may also be the case for several other species. A high level of intraspecific genetic variation have been shown for several widespread and well known Collembola species such as *Isotomurus palustris* (Carapelli et al. 2005), *Orchesella villosa* (Frati et al. 1992) and *Cryptopygus antarcticus* (Stevens et al. 2006) and more recently for *Bilobella aurantiaca, Deutonura monticola, Ceratophysella denticulata, Heteromurus major, Tomocerus baudoti* and *Podura aquatica* (Porco et al. 2012a). Indeed, this high level of cryptic diversity may significantly increase the number of species known, while also providing information on the introduction history in the case of introduced species (Porco et al. 2012a). Given these complex situations of cryptic or molecular diversity, caution should be taken analysing barcoding data, which should be used in complement to traditional taxonomic studies to make accurate biodiversity inventories. Careful consideration is needed to determine these species' status in South Africa. For example, the widespread European species *P. notabilis* (Paclt 1959) has not been found in our collections, although eight endemic species have been found, reiterating the importance of good taxonomic knowledge (Potapov et al. 2011b). In fact, it has recently been found that the well-known and most widespread European species, *Parisotoma notabilis*, has four distinct lineages (Porco et al. 2012c), highlighting the taxonomic challenges ecologists are faced with. Still, the emerging field of phylobetadiversity are opening up exciting possibilities to explore community structures including cryptic diversity (Emerson et al. 2011).

Conclusions

This study has shown, on the basis of extensive sampling, that the Collembolan species richness of the fynbos in southern South Africa is much higher than previously thought. The high endemism, well known for regional flora (Cowling et al. 1992), seems to be reflected among Collembola. Many areas remain unsampled (see Fig. 1) and all microhabitats have not been investigated, thus many species likely remain to be discovered in this region. To understand the diversity of Collembola, I combined the use of traditional taxonomy and modern molecular barcoding techniques, which may help to compensate for the current lack of taxonomic skills. However, rapid progresses in the taxonomic knowledge of South African Collembola through knowledge transfer projects (Janion et al. 2011a) are expected to contribute to the understanding of their role in ecosystem functioning and their response to habitat transformation. This study is an outcome of that knowledge transfer.

Scope of contribution of the candidate

All material collected for this chapter was either collected by the candidate or on fieldwork in which the candidate participated. All of the specimens submitted to the BOLD project were prepared and photographed by the candidate and co-promoter Louis Deharveng. The literature survey was done by the candidate. Sequencing was done by Guelph University (iBOL), while trees were drawn by candidate. Tree construction was undertaken following advice from Bettine Jansen van Vuuren.

References

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In: *Second international symposium on information theory*. B.N. Petrov and F. Czáki (Eds), pp. 267-281. Budapest: Akademiai Kiadó.

Barra, J.-A. (1994) Nouveaux Collemboles Poduromorphes de la Province du Natal (Rép. Sud Africaine) (*Insecta* : *Collembola*). *Journal of Africa Zoology* **108**, 181-189.

Barra, J.-A. (1995) Nouveaux Collemboles Poduromorphes des sables littoraux (partie terrestre) de la Province du Natal (Rép. Sud Africaine) (Insecta : Collembola). *Journal of Africa Zoology* **109,** 125-139.

Barra, J.-A. (1997) Nouveaux Collemboles Entomobryomorphes des sables littoraux (partie terrestre) de la Province du Natal (Rép. Sud Africaine) (Insecta : Collembola). J *Journal of Africa Zoology* **111,** 465-480.

Barra, J.-A (1999) Un nouveau genre *Capbrya* avec deux nouvelles espèces de la Province du Cap (Rep. Sud Africaine) (Collembola : Entomobryidae) *Capbrya* n. gen. D'Afrique du Sud (Insecta : Collembola). *Bulletin de l'Institut Royal des Sceinces naturelles de Belgique. Entomologie* **69,** 19-24.

Barra, J.-A. (2001) *Proisotoma davidi* sp. n. from Cape Province (South Africa) (Collembola). *Mitt. Mus. Nat. kd. Berl., Dtch. Entomol. Z.* **48,** 23-26.

Barra, J.-.A. (2002) Un nouveau genre de Pseudochorutinae (Collembola) des sables littoraux de la Province du Natal (Republique Sud africaine). *Zoosystema* **24,** 177-180.

Barra, J.-A. & Weiner, W.M. (2009) A new species of *Delamarephorura* Weiner & Najt, 1999 (Collembola, Tullbergiidae) from Cape Province (South Africa). *Acta Zoologica Cracoviensia* **52B**, 57-60.

Bellinger, P.F., Christiansen, K.A & Janssens, F. (1996-2012) Checklist of the Collembola of the World. http://www.collembola.org/.

Bengtsson, J., Janion, C., Chown, S.L. and Leinaas, H. P. (2011) Variation in decomposition rates in the fynbos biome, South Africa: the role of plant species and plant stoichiometry. *Oecologia* **165**, 225-235.

Bengtsson, J., Janion, C., Chown, S.L. and Leinaas, H. P. (2012) Litter decomposition in fynbos vegetation, South Africa. *Soil Biology & Biochemistry* **47**, 100-105.

Berlese, J.E (1905) Apparecchio per racogliere press ed in gran numiro piccoli artropodi. *Redia* **2**, 85-89.

Börner, C. (1908) Collembolen aus Sudafrika nebst einer Studie uber die I. Maxille der Collembolen. *In* L. Schultze (Ed.) Forschungensreise im westlischen und zentralen Sudafrika 1903-1905. *Denkschriften der medicinisch-naturwissenschaftlichen Gesellschaft zu Jena* **13,** 58-63.

Börner, C. (1913) Neue Cyphoderinen. *Zoologischer Anzeiger* **41,** 274-284.

Carapelli, A., Frati, F., Fanciulli, P.P., Nardi, F. & Dallai, R. (2005) Assessing species boundaries and evolutionary relationships in a group of south-western species of *Isotomurus* (Collembola, Isotomidae) using allozyme data. *Zoologica Scripta* **34**, 71-79.

Cassagne, N., Gauquelin, T., Bal-Serin, M-C. & Gers, C. (2006) Endemic Collembola, privileged bioindicators of forest management. *Pedobiology* **50**, 127-134.

Chown, S.L. & Froneman, P.W. (2008). *The Prince Edward Islands. Land-Sea Interactions in a Changing Climate*. African Sun Media, Stellenbosch.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2661-2667.

Coates, T.J. (1968a) The Collembola from South Africa – I : The Genus *Neanura*. *Journal of the Entomological Society of southern Africa* **31,** 185-195.

Coates, T. J. (1968b) The Collembola of South Africa – 2: The Genus *Seira*. *The Journal of the Entomological Society of southern Africa* **31**, 435-462.

Coates, T. J. (1969) The Collembola of South Africa – 3: The Genus *Lepidokrugeria*. *Journal of the Entomological Society of southern Africa* **32**, 87-89.

Coates, T.J. (1970) Check-list of the Collembola of South African Parks. *Koedoe* **13**, 181-184.

Cowling, R.M., Holmes, P.M. & Rebelo, A.G. (1992) Plant diversity and endemism. In: *The Ecology of Fynbos: Nutrients, Fire and Diversity*. R.M. Cowling (Ed.), pp. 62-112. Oxford University Press, Cape Town.

Deharveng, L. (1996) Soil Collembola diversity, endemism, and reforestation: a case study in the Pyrenees (France). *Conservation Biology* **10**, 74-84.

Deharveng, L. (2004) Recent advances in Collembola systematics. *Pedobiologia* **48**, 415-433.

Delamare-Deboutteville, C. (1948) Recherches sur les Collemboles termitophiles et myrmécophiles. *Archives de Zoologie expérimentale et générale* **85**, 261-425.

Dippenaar-Schoeman, A.S., González Reyes, A.X., & Harvey, M. (2006) A check-list the Solifugae (sun-spiders) of South Africa (Arachnida, Solifugae). *African Plant Protection* **12**, 70-92.

Dippenaar-Schoeman, A.S & González Reyes, A.X. (2006) South African National Survey (SANSA): Solifugae (sun-spiders) of the national parks and reserves of South Africa (Arachnida, Solifugae). *Koedoe* **49**, 29-38

Emerson, B.C., Cicconardi, F., fanciulli, P.P. & Shaw, P.J.A. (2011) Phylogeny, phylogeography, phylobetadiversity and the molecular analysis of biological communities. *Philosophical Transactions of the Royal Society B* **366**, 2391-2402.

Fiera, C. & Ulrich, W. (2012) Spatial patterns in the distribution of European springtails (Hexapoda: Collembola). *Biological Journal of the Linnean Society* **105,** 498-506.

Fjellberg, A. (2007) *Fauna Entomologica Scandinavica Volume 42. The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona*. Brill, Leiden.

Foord, S.H., Dippenaar-Schoeman, A.S. & Van der Merwe, M. (2002) A check list of the spider fauna of the Western Soutpansberg, South Africa (Arachnida: Araneae). *Koedoe* **45**, 35-43

Frati, F., Fanciulli, P.P. & Dallai, R. (1992) Genetic diversity and taxonomy in soil-dwelling Insects - the genus *Orchesella*. *Journal of Heredity* **83**, 275-281.

Gabriel, A.G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.D., Pugh, P.J.A. & Smith, V.R. (2001) Biological invasions of Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Giliomee, H. & Mbenga, B. (2010) *New History of South Africa*. Tafelberg Publishers, Cape Town.

Godfray, H.C.J. (2002) Challenges for taxonomy. *Nature* **417**, 17-19.

Goto, H. (1953) A species of Collembola, *Sinella coeca* (Schött) (Entomobryidae), new to South Africa. *Entomologist's monthly Magazine* **89**,165-166.

Greenslade, P. The Auquatic Springtails (Insecta: Collembola) of South Africa. http://www.ru.ac.za/static/departments/zoo/Martin/acollembola.html.

Haddad, C.R. & Dippenaar-Schoeman, A.S. (2006) Epigeic spiders (Araneae) in pistachio orchards in South Africa. *African Plant Protection* **12**, 12-22

Hajibabaei, M., Janzen, D.H., Burns, J.M., Hallwachs, W., and Hebert, P.D.N. (2006) DNA barcodes distinguish species of tropical Lepidoptera. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 968-971.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Window 95/98/NT. *Nucleic Acids Symposium Series* **41**, 95-98.

Hebert, P., Ratnasingham, S. & deWaard, J. (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B: Biological Sciences* **270**, S96-S99.

Hlavac, P. (2007) Revision of the subtribe Clavigerodina and an annotated catalogue of South African Clavigeritae (Coleopetera: Staphylinidae: Pselaphinae). *African Invertebrates* **48**, 65-92.

Hogg, I.D. & Hebert, P.D.N. (2004) Biological identification of springtails (Hexapoda: Collembola) from the Canadian Arctic, using mitochondrial DNA barcodes. *Canadian Journal of Zoology* **82**, 749-754.

Holder, M.T. & Lewis, P.O. (2003) Phylogeny Estimation: Traditional and Bayesian Approaches. *Nature Reviews Genetics* **43,** 275-284.

Hopkin, S. (1997) *Biology of the Springtails. Insecta: Collembola*. Oxford University Press, Oxford.

Hugo, E.A., McGeoch, M.A., Marshall, D.J. & Chown, S.L. (2004) Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* **27**, 466-473.

Janion, C., Bedos, A, Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, Liu, A., Malmström, A., Porco, D. & Chown, S.L. (2011a) Springtail diversity in South Africa. *South African Journal of Science* **107**, Art. #582, 7 pages.

Janion, C, Bedos, A., Deharveng, L. (2011b) The genus Ectonura, Cassagnau 1980 in South Africa (Collembola: Neanuridae: Neanurinae), with a key to South African Neanurinae. *ZooKeys* **136**, 31-45.

Janion, C., D'Haese, C. & Deharveng, L. (2012) A new species and first record of the genus *Triacanthella* Schaffer, 1897 (Collembola, Hypogastruridae) for Africa. *ZooKeys* **163**, 57-68.

Janion, C.**,** Leinaas, H.-P., Terblanche, J.S., & Chown, S.L. (2010) Trait means and reaction norms: the consequences of climate change/invasion interactions at the organism level. *Evolutionary Ecology* **24**, 1365-1380.

Janion, C.**,** Worland, R.M. & Chown, S.L. (2009) Assemblage level variation in lower lethal temperature: the role of invasive species on sub-Antarctic Marion Island. *Physiological Entomology* **34**, 284-291.

Jinbo, U., Kato, T. & Ito, M. (2011) Current progress in DNA barcoding and future implications for entomology. *Entomological Science* **14**, 107-124.

Jordana, R. (2012) *Synopses on Palearctic Collembola. Capbryinae & Entomobryini*. W. Dunger & U. Burkhardt (Eds). Museum of Natural History, Görlitz.

Kim, K. C. (1993) Biodiversity, conservation and inventory: Why insect matter. *Biodiversity and Conservation* **2**, 191-214.

Lawrence, R.F. (1953) *The biology of the cryptic fauna of forest. With special reference to the indigenous forest of South Africa*. Balkema: Cape Town.

Linnæus, C. (1758) *Systema natura per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Pp. 1-812. Holmiæ, Salvius.

Liu, A., Janion, C. and Chown, S.L. (2012) Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations. *Pedobiologia* **55**, 203-209.

Nillsson-Örtman, V. & Nilsson, A.N. (2010) using taxonomic revision data to estimate species richness and characteristics of undescribed species of diving beetles (Coleoptera: Dytiscidae). *Biodiversity Informatics* **7**, 1-16.

Paclt, J. (1959) *Collembola. South African Animal Life*. Results of the Lund University Expedition in 1950-1951. Vol. VI, p. 24-78.

Paclt, J. (1964) Ein neuer *Prorastriopes* aus Zululand und zur Nomenklatur due südafrikianischen *Rastropes*-Art. *Senck. Boil.* **45**, 661-663.

Paclt, J. (1965) *Cyphoderus trinervoidis* n.sp., ein neuer Termitophile aus Transvaal (Ins., Collembola). *Senck. Boil*. **46**, 59-60.

Pactl, J. (1967) On South and Central African Collembola. *Journal of the Entomological Society of southern Africa* **29,** 135-47.

Parr, C.L., Robertson, H.G. & Chown, S.L. (2003) Apomyrminae and Aenictogitoninae: two new subfamilies of ant (Hymenoptera: Formicidae) for southern Africa. *African Entomology* **11**, 128-129.

Petersen, H. & Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* **39**, 287-388.

Porco, D., Bedos, A., and Deharveng, L. (2010a) Description and DNA barcoding assessment of the new species *Deutonura gibbosa* (Collembola: Neanuridae: Neanurinae), a common springtail of Alps and Jura. *Zootaxa* **2639**, 59-68.

Porco, D., Bedos, A., Greenslade, P., Janion, C. , Skarżyński, D Stevens, M., Jansen van Vuuren, B. & Deharveng, L. (2012a) Challenging species delimitation in Collembola: cryptic diversity among common springtails unveiled by DNA barcoding. *Invertebrate Systematics* **26**, 470-477.

Porco, D., Decaëns, T., Deharveng, L., James, S.W., Skarńynski, D., Erséus, C., Butt, K.R., Richard, B. & Hebert, P.D.N. (2012b) Biological invasions in soil: DNA barcoding as monitoring tool in a multiple taxa survey targeting European earthworms and springtails in North America. *Biological Invasions*, in press.

Porco, D., Potapov, M., Bedos, A., Busmanchiu, G., Weiner, W.M., Hamra-Kroua, S. and Deharveng, L. (2012c) Cryptic diversity in the ubiquist species *Parisotoma notabilis* (Collembola, Isotomida): a long-used chimeric species? *Plos ONE* **7**, e46056.

Porco, D., Rougerie, R., Deharveng, L. & Hebert, P. (2010b) Coupling non-destructive DNA extraction and voucher retrieval for small soft-bodied Arthropods in a high-throughput context: the example of Collembola. *Molecular Ecology Resources* **10**, 942-945.

Potapov, M., Bu, Y. & Gao, Y. (2011a) First record of the littoral family Isotogastruridae (Collembola) in Asia. *ZooKeys* **136**, 23–29.

Potapov, M., Janion, C. & Deharveng, L. (2011b) Two new species of *Parisotoma* (Collembola: Isotomidae) from the Western Cape, South Africa. *Zootaxa* **2771**, 17-24.

Posada, D. (2008) jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* **25**, 1253-1256.

Qu, J.Q., Zhang, F. & Chen, J.X. (2010) Two new species of the genus *Sinella* Brook, 1882 (Collembola: Entomobryidae) from East China. *Journal of Natural History* **44**, 2535-2541.

Ratnashingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes* **7**, 355-364.

Robertson, H.G. (2000) Afrotropical ants (Hymenoptera: Formicidae): taxonomic progress and estimation of species richness. *Journal of Hymenoptera Research* **9**, 71-84.

Robertson, H.G. (2002) Revision of the ant genus *Streblognathus* (Hymenoptera: Formicidae: Ponerinae). *Zootaxa* **97**, 1-16.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayers 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19** , 1572-1574.

Rusek, J. (1998) Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation* **7**, 1207-1219.

Samper, C. (2004) Taxonomy and environmental policy. *Philosophical Transactions of the Royal Society of London B* **359**, 721–728.

Samways, M.J., McGeoch, M.A. & New, T.R. (2010) *Insect Conservation. A handbook of Approaches and Methods*. Oxford University Press Inc., New York.

Schlettwein, C.H.G. & Giliomee, J.H. (1987) Comparison of insect biomass and community structure between fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. *Annale Universiteit van Stellenbosch* **Series A3 Vol. 2**, 1-76.

Snider, R.J. (1988) *Tritosminthurus schuhi*, a new genus and species from Cape Province, South Africa (Collembola: Bourletiellidae). *Entomological News* **99,** 260-266.

Stevens, M.I., Fjellberg, A., Greenslade, P., Hogg, I.D. & Sunnocks, P. (2006) Redescription of the Antarctic springtail *Desoria klovstadi* using morphological and molecular evidence. *Polar Biology* **29**, 820-830.

Terauds, A., Chown, S.L. & Bergstrom, D.M. (2011) Spatial scale and species identity influence the indigenous-alien diversity relationship in springtails. *Ecology* **92,** 1436-1447.

Tullgren, A. (1918) Ein sehr einfacher Ausleseapparat fur terricole Tierformen. *Zeitschrift Fur Angewante Entomologie* **4**, 149-150

Ulrich, W. & Fiera, C. (2009) Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologia* **35**, 45-52.

Ulrich W. & Fiera C. (2010) Environmental correlates of body size distributions of European springtails (Hexapoda: Collembola). *Global Ecology & Biogeography* **19,** 905-915.

Wallace, M.M.H. (1964) Present and probable world distribution of *Sminthurus viridis* and prospects for its biological control. *Pedobiologia* **14**, 238-243.

Wallace, M.M.H. & Walters, M.C. (1974) The introduction of *Bdellodes lapidaria* (Acari: Bdellidae) from Australia into South Africa for the biological control of *Sminthurus viridis* (Collembola). *Australian Journal of Zoology* **22**, 505-517.

Walters, M.C. (1968) A study of *Sminthurus viridis* (L.) (Collembola) in the Western Cape Province. *Entomol Mem. Dep. Agric. S. Afr.* **16**.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629-1633.

Weiner, W.M. & Najt, J. (1991) Collembola Poduromorpha of South Africa. *Bonn. Zool. Beitr*. **42,** 369-387.

Weiner, W.M. & Najt, J. (1998) Collembola (Entognatha) from East Africa. *European Journal of Entomology* **95,** 217-237.

Weiner, W.M. & Najt, J. (1999) New genus of Tullbergiinae (Collembola). *Annales de la Société entomologique de France* **35**, 183-187.

Womersley, H. (1931) Some Collembola of the family Sminthuridae from South Africa. *Annals of the South African Museum* **30,** 137-156.

Womersley, H. (1934) On some Collembola—Arthropleona from South Africa and Southern Rhodesia. Annals of the South African Museum **30,** 441–475.

Yosii, R. (1959) Collembola fauna of the Cape Province, with special reference to the genus *Seira*. *Biological results from the Japanese Antarctic Research Expeditions* **6,** 3-24.

Zhang, F., Chen, J.X. & Deharveng, L. (2011) New insight into the systematics of the *Willowsia* complex. *Annales de la Société entomologique de France* **47**, 1-20.

Tables

Table 1: A summary of the Collembola species recorded from the Western Cape through DNA barcoding, literature and from our sampling.

Order	Family	No. species from literature	No. species from literature accepted	No. endemics from literature	No. introduced from literature	No. species in our samples	**Total for Western Cape**
Entomobryomorpha	Cyphoderidae	1	1	1	0	1	**2**
	Entomobryidae	27	21	15	6	41	**62**
	Isotomidae	12	10	5	5	36	**46**
	Microfaculidae	0	0	0	0	1	**1**
	Tomoceridae	1	1	1	0	1	**2**
	Oncopoduridae	0	0	0	0	1	**1**
	Paronellidae	0	0	0	0	1	**1**
	Total	**41**	**33**	**22**	**11**	**82**	**115**
Neelipleona	Neelidae	1	1	0	1	2	**3**
	Total	**1**	**1**	**0**	**1**	**2**	**3**
Poduromorpha	Brachystomellidae	6	6	5	1	4	**10**
	Hypogastruridae	13	8	2	6	8	**16**
	Isotogastruridae	0	0	0	0	1	**1**
	Neanuridae	10	9	6	3	19	**28**
	Odontellidae	1	1	1	0	4	**5**
	Onychiuridae	3	1	1	0	3	**4**
	Tullbergiidae	3	2	1	1	10	**12**
	Total	**36**	**27**	**16**	**11**	**49**	**76**
Symphypleona	Arrhoplaitidae	0	0	0	0	1	**1**
	Bourletiellidae	4	4	4	0	2	**6**
	Dicyrtomidae	2	2	1	1	1	**3**
	Katiannidae	3	3	2	1	2	**5**
	Mackenziellidae	0	0	0	0	1	**1**
	Sminthuridae	1	1	0	1	1	**2**
	Sminthurididae	1	1	0	1	1	**2**
	Total	**11**	**11**	**7**	**4**	**8**	**19**
TOTAL		**89**	**72**	**45**	**27**	**141**	**213**

Figures

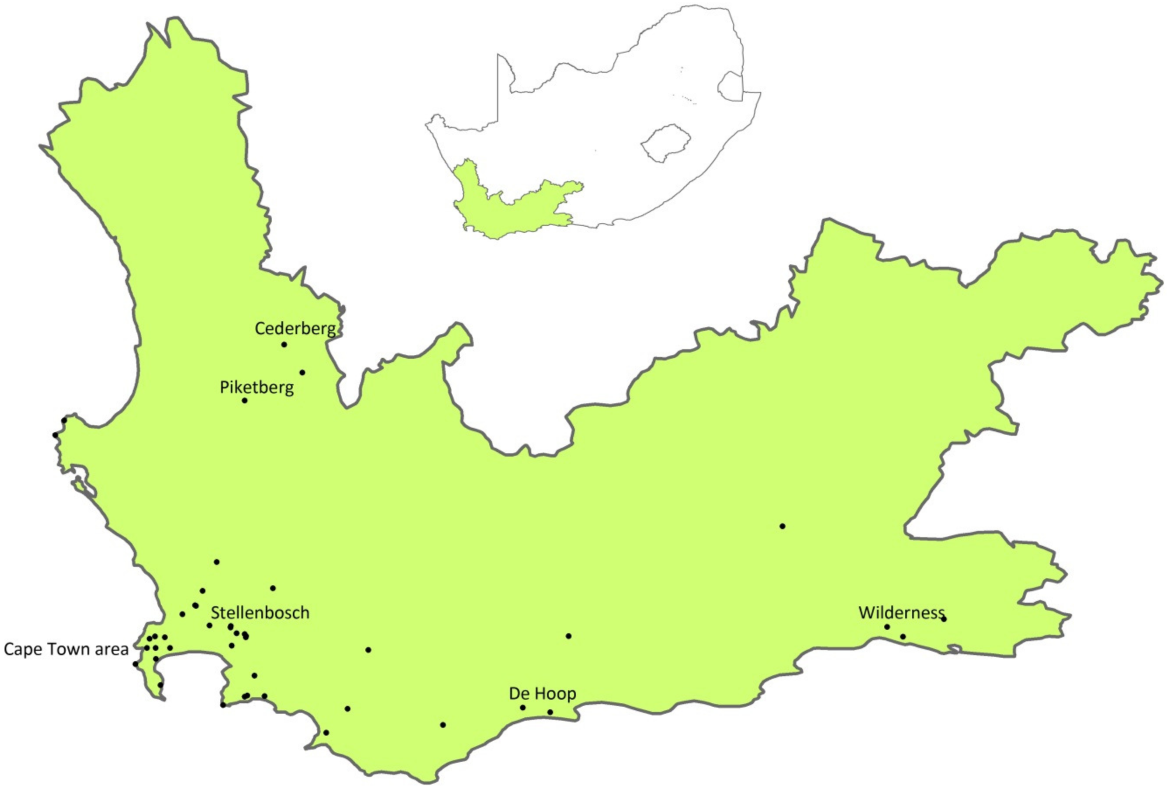


Figure 1: Map indicating the sampling sites in the Western Cape Province. Map by B. Coetzee.

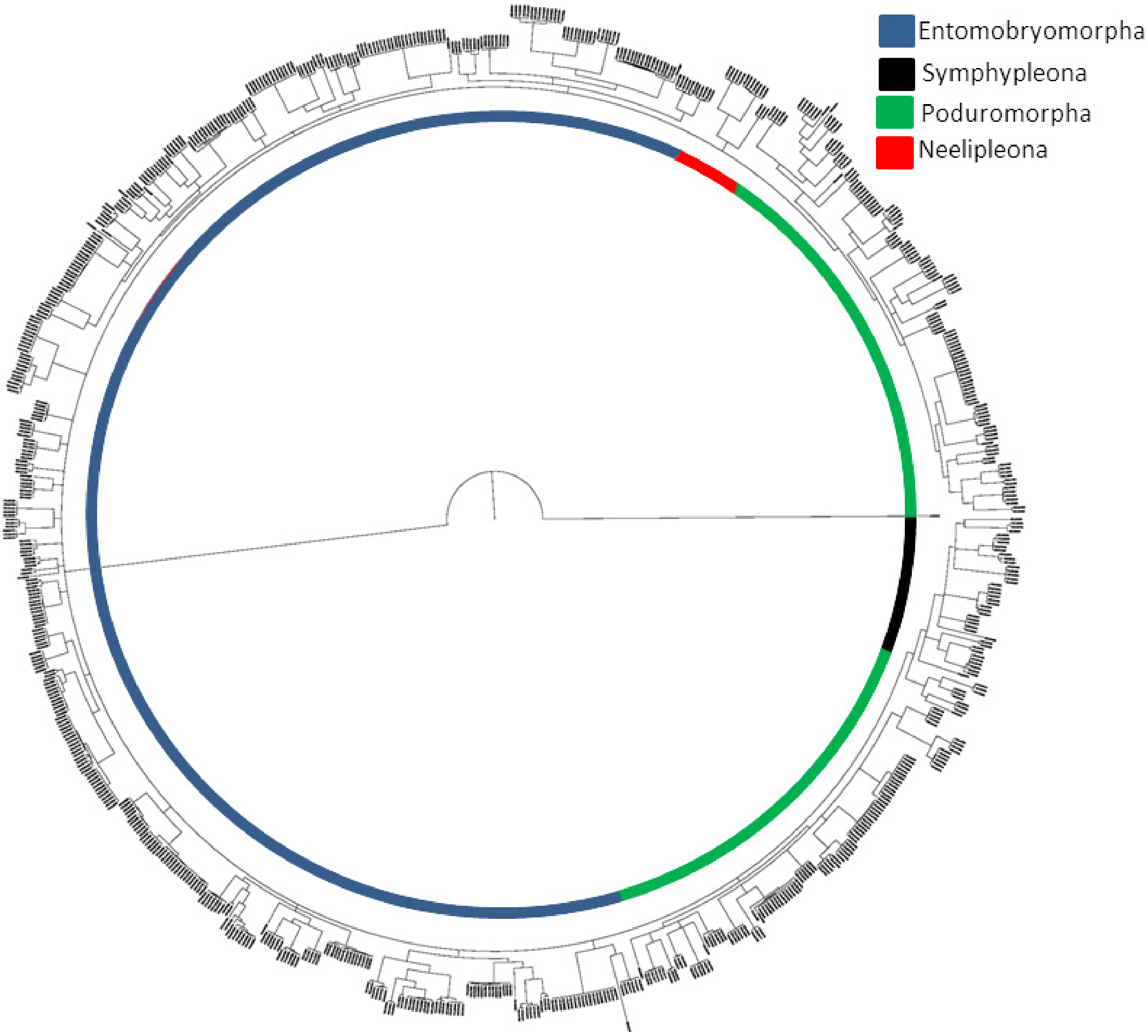


Figure 2: The Bayesian Inference consensus tree indicating the evolutionary diversity of all Collembola sampled from the Western Cape. The consensus tree is based on a 658-bp fragment of the mitochondrial cytochrome oxidase I (COI) gene.

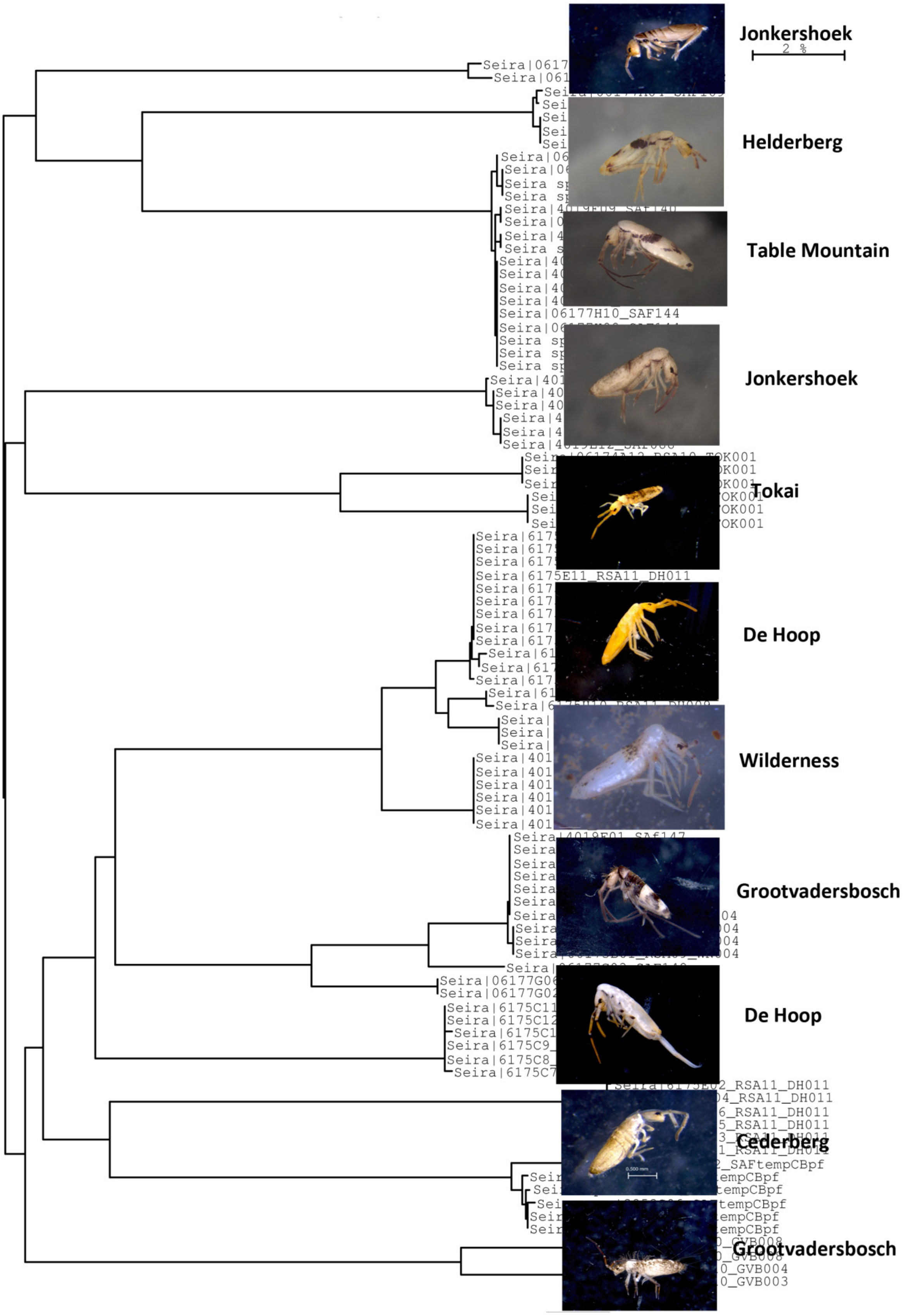

Jonkershoek
2 %
Helderberg
Table Mountain
Seira|06177H10_SAF144
Jonkershoek
Tokai
Seira|6175E11_RSA11_DH011
De Hoop
Wilderness
Grootvadersbosch
De Hoop
Cederberg
Grootvadersbosch

Figure 3: Taxon ID tree of *Seira* species from the Western Cape illustrating the different colour patterns found in this genus.

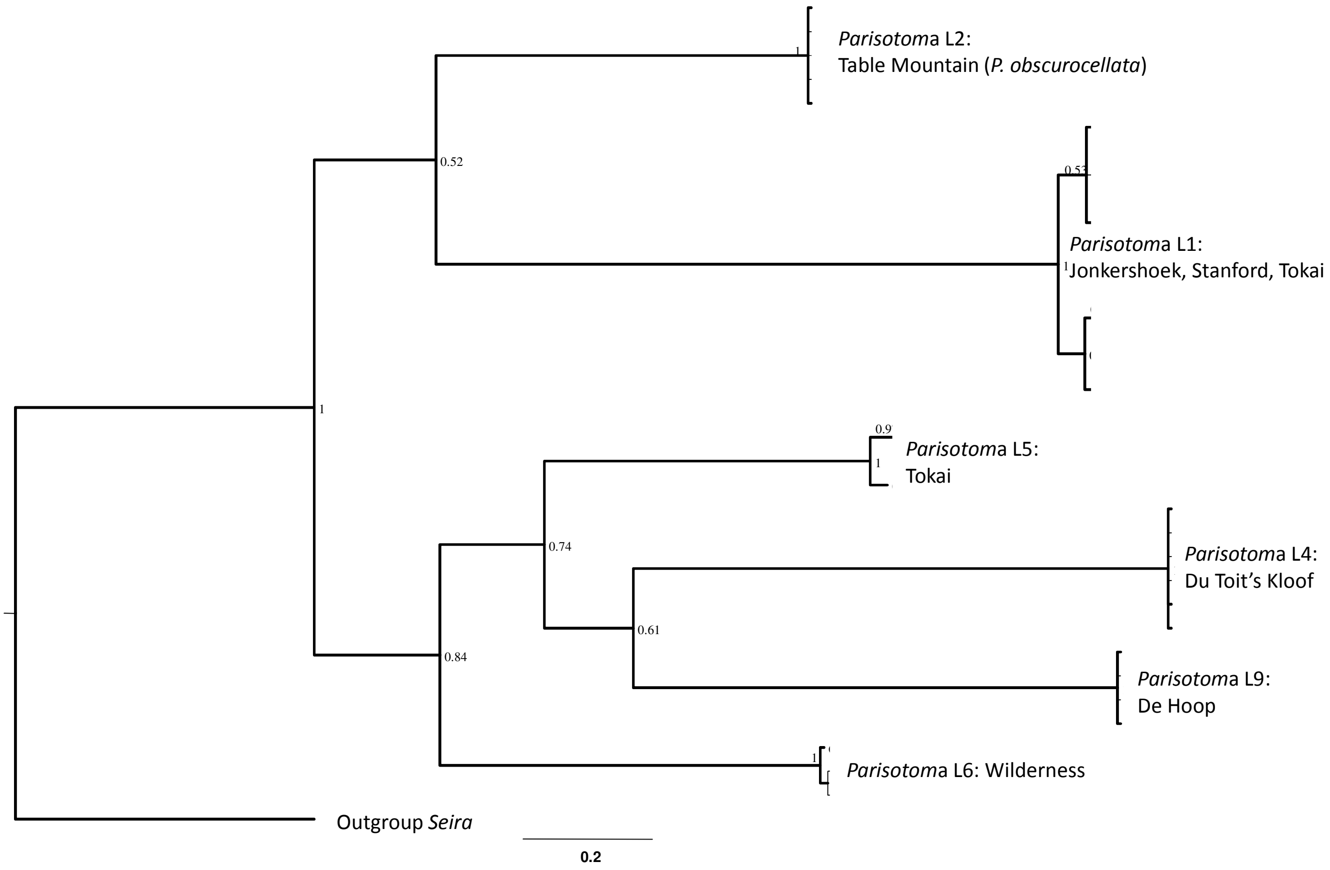


Figure 4: Taxon ID tree of all *Parisotoma* barcoded from the Western Cape. Posterior probabilities (from Bayesian Inference analyses) supporting nodes are shown. The posterior probabilities values above 0.90 are shown at the nodes, and values of ≥ 0.95 are considered as significant (bar = 0.2).

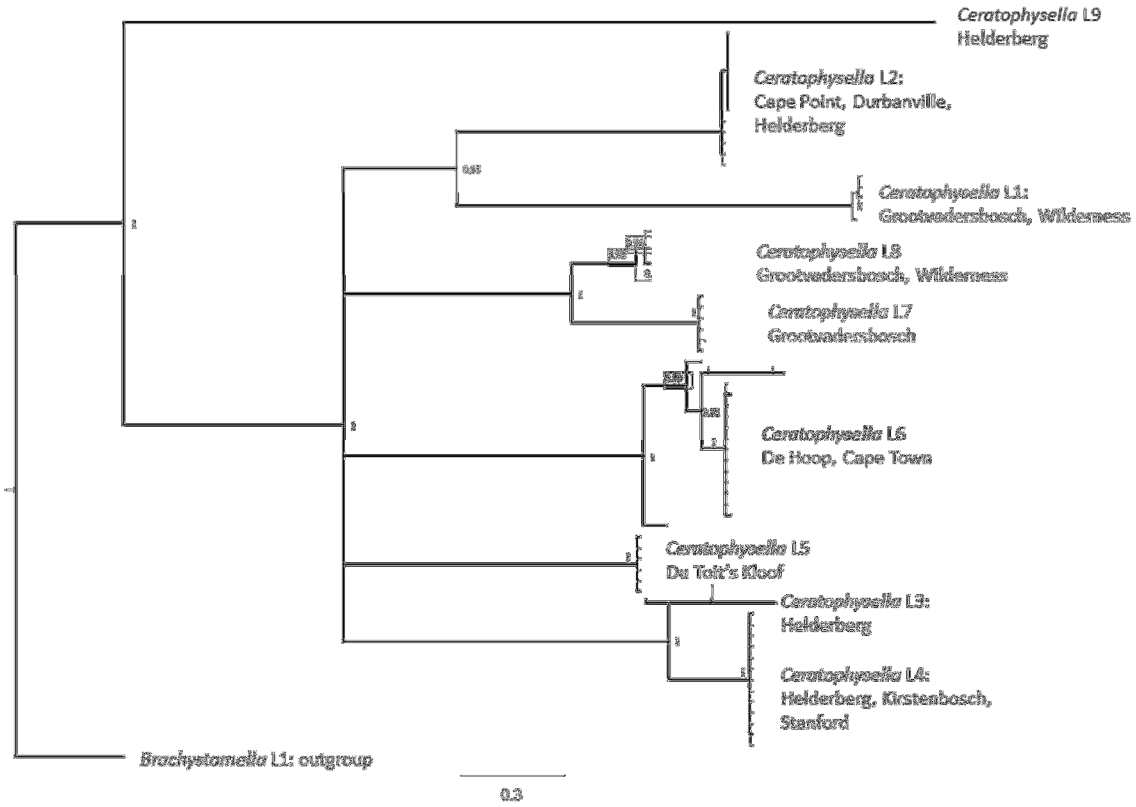


Figure 5: Taxon ID tree of the all *Ceratophysella* species barcoded for the Western Cape. The posterior probabilities values above 0.90 are shown at the nodes, and values of ≥ 0.95 are considered as significant (bar = 0.3).

Supplementary material

Table 1: All species recorded and described from South Africa. **Abbreviations used:** South Africa (SA); Western Cape (WC); Eastern Cape (EC); Kwazulu-Natal (KZN); Gauteng (G); Limpopo (L); Free State (FS); Northern Cape (NC); Mpumalanga (MP); North West Province (NWP), endemic (E), introduced (I), widely distributed in the tropics (PT), juv – juvenile specimen(s); ♂ - male; ♀- female, questionable identification - ?. ISEA - Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland; ISNB- l' Institut Royal des Sciences Naturelle de Belgique; MNHN - Museum national d'Histoire naturelle, Paris, France; MSPU - Moscow State Pedagogical University, Russia; Museum Lund – Museum of Lund; NIC - National Insect Collection, Pretoria; RMCA - Royal Museum of Central Africa at Tervuren, Belgium / Musee royal d'Afrique centrale Tervuren, Belgique; SAMC - South African Museum, Cape Town ; SAMA - South Australian Museum, Adelaide, Australia. Endemic genera are indicated by an asterisk (*). Collection numbers or codes are given as in the publications.

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
PODUROMORPHA						
Brachystomellidae						
Brachystomella coatesi Weiner and Najt, 1991	Weiner and Najt 1991	WC	E	Type locality: Saasveld, near George, subtropical indigenous forest, pitfall traps, 17.xii.1986-17.i.1987, V. Nicolai leg	Holotype ♀, paratypes 1 ♂ juv, 10 ♀, 6 juv (ISEA), paratypes 7 ♀, 4 juv, (MNHN)	
Brachystomella georgensis Weiner and Najt, 1991	Weiner and Najt 1991	WC	E	Type locality: Saasveld, near George, subtropical indigenous forest, pitfall traps, 17.xii.1986-17.i.1987, V. Nicolai leg	Holotype ♀, paratypes 2 ♀, 2 juv (ISEA), paratypes 1 ♀, 2 juv, (MNHN)	
Brachystomella parvula africana Yosii, 1959	Yosii 1959	WC	E?	Kloofnek, 4.xii.1957, 12 specimens.		*B. africana* on www.collembola.org
Brachystomella parvula (Schäffer, 1896)	Coates 1970	MP	I	Kruger National Park, under rotting leaves of *Bougainvillea* sp. and under *Portulacaria afra*, Shingwidzi Rest Camp; under *Hyphaene crinita*, Shingwidzi River.		Cosmopolitan distribution according to Fjellberg (1998).
Brachystomella parvula (Schäffer, 1896)	Paclt 1967	WC	I	Van Rhynsdorp Knersvlakte, 3 miles from Van Rhyns Pass, 22.iii.1956, 75 specimens AcV93; Muisenberg Boyes Drive Waterfall, damp soil and moss, 15.iv.1956, 1 specimens AcV98; Kalk Bay, Boyes Drive, damp soil, 22.iv.1956, 1 specimen AvC100, Simons Town, Red Hill Drive, damp soil and moss, 22.iv.1956, 4 specimens AcV101, Table Mountain Drive waterfall, damp soil and moss, 5.v.1956, 12 specimens AcV104, Ibidem, Table Mountain Drive, humus and pine needles, 5.v.1956, 7 specimens AcV105, all material D.v.V. Webb leg.	NIC	Cosmopolitan distribution according to Fjellberg (1998).
Brachystomella parvula (Schäffer, 1896)	Paclt 1959	WC	I	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.12.1950 Loc. 79 (61 specimens), Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.1.1951 loc. 161 (14 specimens) (all SSAE leg.).	All specimens Museum Lund	Cosmopolitan distribution according to Fjellberg (1998).

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Brachystomella parvula (Schäffer, 1896)	Paclt 1959	KZN	I	Pietermaritzburg, from dry leaves in garden, Sept 1951, 12 specimens, Champagne Castle, Drakensberg, Feb 1946, 6 specimens, R.F. Lawrence leg.		Cosmopolitan distribution according to Fjellberg (1998).
Brachystomella parvula (Schäffer, 1896)	Paclt 1959	EC	I	Dordrecht district, from heap of decomposing mealie cobs, July and October 1957, 20 specimens, R. van Pletzen leg.		Cosmopolitan distribution according to Fjellberg (1998).
Brachystomella parvula (Schäffer, 1896)	Paclt 1959	FS	I	Fouriesburg, surface of rain pool, Jan or April 1957, about 270 specimens, Bloemfontein, under few pine trees, from soil containing large amounts of organic material, April 1957, 1 specimen, Bloemfontein, garden, soil with large amounts of organic plant material, 11 specimens, R. van Pletzen leg.		Cosmopolitan distribution according to Fjellberg (1998).
Brachystomella parvula (Schäffer, 1896)	Womersley 1934	WC	I	Burghersdorp, Jan. 1913 Robertson leg, Cape Town, 9 May 1916 (K.H. Barnard leg), Elsenberg, 24 July 1920 (Womersley leg), Rondebosch C.P. July 1930 (Womersley leg), Kloof Nek, 3.viii.1930 (Womersley leg), Stellenbosch, 19 Aug. 1920 (Womersley leg)		Cosmopolitan distribution according to Fjellberg (1998).
Brachystomella sp. Ågren, 1903	Lawrence 1953	?	?	No information given.		
Probrachystomellides nicolaii Weiner and Najt, 1991*	Weiner and Najt 1991	WC	E	Type locality: Saasveld, near George, subtropical indigenous forest, pitfall traps, 17.xii.1986-17.i.1987, V. Nicolai leg.	Holotype ♀, paratypes 9 females, 5 ♂, 11 juv (ISEA), paratypes 11 ♀, 3 males, 8 juv, (MNHN)	
Setanodosa capitata (Womersley, 1934)	Womersley 1934	WC	E	Stellenbosch, 12.viii.1930 (Womersley leg), Cape Town June 1915 (K.H. Barnard leg).	Co-types in SAMC	*Brachystomella capitata* Womersley, 1934
Hypogastruridae						
Acherontiella thibaudi Barra, 1994	Barra 1994	KZN	E	Type locality: Sodwana Bay National Park, KwaZulu-Natal, 300 km N of Durban, foot of the dune at top of beach, humid sand at 20 cm depth, under low pioneer vegetation, J.-P. Rieb leg.	Holotype male and one paratype ♀ in RMCA, paratype ♂ at MNHN, Paris,	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					other paratypes with Barra	
Austrogastrura lobata (Yosii, 1959)	Yosii 1959	WC	E	Table Mountain, 11.iii.1958, 2 ♂ examined.		*Choreutinula lobata* Yosii, 1959
Ceratophysella armata (Nicolet, 1842)	Paclt 1959	WC	?	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 Loc. 79, Wynberg Cave Ravine, sieved from wet vegetable debris, 2400 ft, 18.xii.1950, Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.i.1951 loc. 161 (all SSAE leg.)	Thousands of specimens Museum Lund	*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1959	KZN	?	Drakensberg 8 miles ENE from Rhodes, on stony ericaceous heath, alt 8000 ft., 9.iii.1951 SSAE leg, loc. 223.	16 specimens Museum Lund	*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to *H. armata* are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1959	EC	?	Dordrecht district, from heap of decomposing mealie cobs (about 180 specimens), July and October 1957, R. van Pletzen leg., also small poplar grove from soil containing decomposing leaves.		*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1959	FS	?	Fouriesburg, surface of rain pool, Jan or April 1957, about 1800 specimens, Bloemfontein, under few pine trees, from soil containing large amounts of organic material, April		*Hypogastrura armata* Nicolet, 1842, dubious, old

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				1957 (1 specimen), Bloemfontein, garden, soil with large amounts of organic plant material, April 1957 (5 specimens) - all R. van Pletzen leg.		Nordic references referring to *H. armata* are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1959	G	?	Johannesburg, 10.iii.1958, SA Institute for Medical Research leg., (140 specimens).		*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1967	G	?	Louis Trichardt, surface of pools of standing water, 3.viii.1939 (20 specimens AcV63); Idem, Elim Hospital, surface of pools of standing water, 3.viii.1939, 70 specimens AcV64 (all T. Kelly leg), Krugersdorp District, Blyvooruitsig, damp garden soil, 29.ii.1956, 20 specimens AcV65; 7 specimens AcV88, D.B. Wells leg.	NIC	*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1967	WC	?	Mamre Road, Waterkloof Farm, July 1937, 3 specimens AcV30Gordons Bay, 9.viii.1937, 14 specimens AcV35, 10.viii.1937, 3 specimens AcV38, 11.viii.1937, AcV40 and 13.viii.1937, 18 specimens AcV43; Velddrift, damp soil along banks of Berg River, 20.iii.1956, 16 specimens AcV90, Muizenberg, Boyes Drive Waterfall, damp soil and moss, 15.ix.1956, 9 specimens AcV98, Hout Bay, Chapman's Peak Drive, damp soil and moss, 22.iv.1956, 23 specimens AcV102, Table Mountain Drive Waterfall, damp soil and moss, 5.v.1956, 27 specimens AcV104, Idem, Table	NIC	*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				Mountain Drive, humus and pine needles, 5.v.1956, 7 specimens AcV105 (all material D.v.V. Webb leg.).		
Ceratophysella armata (Nicolet, 1842)	Womersley 1934	KZN	?	Inchanga, Nov. 1917, K.H. Barnard leg.		*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Womersley 1934	NC	?	Langklip Siding, Gordonia C.P. Aug. 1925, H.K. Barnard leg.		*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Womersley 1934	WC	?	Stellenbosch 24 .vii.1930, 12.viii.1930, H.W. leg., Kloofnek, 27.viii.1930 (H.W. leg), Stellenbosch C.P. 28.viii.1927 (A.J. Hesse).		*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Coates 1970	EC	?	Addo Elephant National Park, on reeds and also in soil, Caesar's dam.		*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H.

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
						armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata (Nicolet, 1842)	Paclt 1967	NC	?	Upington, banks of Orange River, Dec 1937, 2 specimens, AcV49 and 3 specimens AcV52, Graaff-Reinet 24.ix.1939, 3 specimens AcV71 and 29.ix.1939 1 specimens AcV73, D.v.V. Webb leg.	NIC	*Hypogastrura armata* Nicolet, 1842, dubious, old Nordic references referring to H. armata are of *Ceratophysella denticulata* (Fjellberg 1998)
Ceratophysella armata var. *trispina* Womersley, 1934	Womersley 1934	WC	?	Stellenbosch, 1927, A.J. Hesse leg.	Type in SAMC	*Hypogastrura armata trispina* Womersley, 1934. Dubious: only one speciemen available with three anal spines, could also have been *Triacanthella* sp.
Ceratophysella longispina (Tullberg, 1876)	Womersley 1934	NC	?	Langklip Siding, Gordonia, Aug 1925, K.H. Barnard leg.		*Hypogastrura longispina* Tullberg, 1876 Misidentification: considered a circumpolar species by Fjellberg (1998) occurring in wet tundra habitats.
Ceratophysella longispina (Tullberg, 1876)	Womersley 1934	KZN	?	Ichanga, Nov 1917, K.H. Barnard leg.		*Hypogastrura longispina* Tullberg, 1876

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
						Misidentification: considered a circumpolar species by Fjellberg (1998) occurring in wet tundra habitats.
Hypogastrura manubrialis var. *neglectus* (Börner, 1901)	Womersley 1934	WC	?	Stellenbosch, 29.viii.1930 Womersley leg.		Dubious: lacks two anal spines, no more information provided.
Hypogastrura manubrialis (Tullberg, 1876)	Paclt 1959	NC	I	Kimberley.		
Hypogastrura manubrialis (Tullberg, 1876)	Paclt 1967	KZN	I	Durban, African Mushroom Industries Ltd., 15.viii.1939, 90 specimens.	NIC	
Hypogastrura manubrialis (Tullberg, 1876)	Womersley 1934	NC	I	Kimberley, Feb 1915, Miss Wilman leg.		
Hypogastrura manubrialis (Tullberg, 1876)	Womersley 1934	WC	I	Elsenburg 24.vii.1930, Rondebosch, C.T., 29.vii.1930, Stellenbosch, 24.vii.1930 and 29.viii.1930.		
Hypogastrura purpurescens (Lubbock, 1868)	Paclt 1967	WC	I	Paarl, fallen leaves, 29.vii.1937, 1 specimen AcV29, D.v.V. Webb leg.	NIC	Considered a cosmopolitan species by Fjellberg (1998)
Hypogastrura purpurescens (Lubbock, 1868)	Paclt 1959	WC	I	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950, SSAE leg, Loc. 79.	3 specimens, Museum Lund	Considered a cosmopolitan species by Fjellberg (1998)
Hypogastrura purpurescens (Lubbock, 1868)	Womersley 1934	WC	I	Outskirts of Cape Town, Womersley leg, 24.viii.1930.		Considered a cosmopolitan species by Fjellberg (1998)
Hypogastrura sahlbergi (Reuter, 1895)	Paclt 1959	WC	I	Franschhoek Bosreserve, Upper Berg river, at stream, alt 1500 ft., 1.xi.1950, SSAE leg, loc 21.	1 specimen Museum Lund	
Hypogastrura sahlbergi var. *rosea* (Reuter, 1895)	Womersley 1934	WC	?	Near top of Lion's Head, Cape Town, on damp rocks, 3.viii.1930, Womersley leg.		Dubious: agree with type except for

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
						colour.
Hypogastrura sp. Bourlet, C. 1839:404	Lawrence 1953	?	?	No information given.		
Hypogastrura viatica (Tullberg, 1872)	Paclt 1959	WC	I	Seapoint, Cape Town, Carpenter leg.		Considered a cosmopolitan species by Fjellberg (1998).
Hypogastrura viatica (Tullberg, 1872)	Womersley 1934	WC	I	Sea Point, Cape Town, shore pools, Sept 1929 Prof. W. D'Arcy Thompson leg.		Considered a cosmopolitan species by Fjellberg (1998).
Mesogastrura libyca (Caroli, 1914)	Paclt 1959	WC	I	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 Loc. 79 (64 specimens), Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.1.1951 (74 specimens), loc. 161 all SSAE leg.	Museum Lund	*Choreutinula libyca* Caroli, 1914 Cosmopolitan distribution (Fjellberg 1998).
Schaefferia sp. Absolon, K, 1900:265	Sharratt et al. 2000	WC	?	Table Mountain Peninsula caves, bat guano.		Dubious: probably *Triacanthella madiba* Janion, D'Haese and Deharveng, 2012
Willemia trilobata Barra, 1995	Barra 1995	KZN	E	Type locality: Sodwana Bay, foot of the dune at top of beach, humid sand at 20 cm depth, under low pioneer vegetation, 03.ii.1992, J.-P. Rieb leg.	Holotype ♂ and ♀ paratype, RMCA	
Xenylla capensis Weiner and Najt, 1991	Weiner & Najt 1991	WC	E	Type locality: Saasveld, near George, subtropical indigenous forest, pitfalls, 17.xii.1986-17.i.1987, V. Nicolai leg.	Holotype ♀, paratypes 2 ♂, 3 ♀, 6 juv, (ISEA), paratypes 2 ♀, 1 ♂, 2 juv (MNHN)	
Xenylla maritima Tullberg, 1869	Paclt 1959	WC	I	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950, loc. 79 (45 specimens), Table Mountain, Wynberg Cave Ravine, sieved from wet debris, 2400ft, 18.xii.1950 loc 84 (5 specimens), Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600ft, 28.i.1951, loc.161 (18 specimens),	Museum Lund	Cosmopolitan distribution (Fjellberg 1998)

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				all SSAE leg., (Cape Town, on pods June 1915 K.H. Barnard leg. from Womersley slide).		
Xenylla maritima Tullberg, 1869	Paclt 1959	EC	I	Dordrecht district, from heap of decomposing mealie cobs (about 180 specimens), July and October 1957, R. van Pletzen leg., also small poplar grove from soil containing decomposing leaves, a population of about 2500 specimens		Cosmopolitan distribution (Fjellberg 1998)
Xenylla maritima Tullberg, 1869	Paclt 1959	KZN	I	Drakensberg, Champagne Castle, Feb 1946, R.F. Lawrence leg, 1 specimen.		Cosmopolitan distribution (Fjellberg 1998)
Xenylla maritima Tullberg, 1869	Paclt 1967	NWP	I	Marico District, fallen leaves, 13.i.1930, one specimen AcV3, J.C. Faure leg.	NIC	Cosmopolitan distribution (Fjellberg 1998)
Xenylla maritima Tullberg, 1869	Paclt 1967	WC	I	Mamre Road, Waterkloof Farm, 3.vii 1937, 5 specimens AcV28 and July 1937, 46 specimens AcV30; Velddrift, damp soil along banks of Berg River, 20.iii.1956, 1 specimen AcV90; Van Rhynsdorp Knersvlakte, 3 miles from Van Rhyns Pass, 22.iii.1956, 2 specimens AcV93; Kalk Bay, Boyes Drive, damp soil, 22.iv.1956, 1 specimen AvC93, Rosebank, Entomology Research Station, damp soil and moss, 24.ix.1956, 6 specimens AcV103, Table Mountain Drive, humus and pine needles, 5.v.1956, 1 specimen AcV105, all material D.v.V. Webb leg.	NIC	Cosmopolitan distribution (Fjellberg 1998)
Xenylla maritima Tullberg, 1869	Womersley 1934	WC	I	Stellenbosch – 12.xiii.1930, Fish Hoek – 23.viii.1930, Hout Bay - Aug 1930 (Womersley leg.)		Cosmopolitan distribution (Fjellberg 1998)
Xenylla rhodesiensis Womersley, 1926	Coates 1970	MP	PT	Kruger National Park, under reeds in vlei, Klopperfontein No. 151.		
Xenylla schillei Börner, 1903	Paclt 1959	Lesotho	I	Qachas Nek, at small stony stream surrounded by grassy meadow, alt 6500 ft., 7.iii.1951, SSAE leg, loc. 213	1 specimen Museum Lund	Dubious, as this species has only been recorded from Europe, while the

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
						collection locality is also very isolated and at a high altitude.
Xenylla sp. Tullberg, 1869	Lawrence 1953	?	?	No information given.		
Xenylla yucatana Mills, 1938	Barra 1995	KZN	PT	Sodwana Bay dense shrub forest, sand thin humus layer, 02.ii.1992, J-P Rieb leg.	RMCA	
Neanuridae						
Aethiopella flavoantennata capensis (Womersley, 1934)	Womersley 1934	WC	E	Slopes of Table Mountain, Cape Town, 5.viii.1919, K.H.B. leg, 29.viii.1930, Womersley leg.		*Ceratrimeria flavoantennatus* Womersley, 1934
Aethiopella flavoantennatus capensis Womersley, 1934	Womersley 1934	KZN	E	Inchanga, Nov. 1917, K.H.B. leg.		
Aethiopella flavoantennatus capensis Womersley, 1934	Paclt 1959	WC	E	Bainskloof, 10 miles east of Wellington, at stony stream, mountain slope, 1.vii.1951, SSAE leg, - Ibidem, under stones on sandy ground, alt 6800 ft., 1.vii. 1951, SSAE leg, loc. 346.	2 specimens Museum Lund, Ibidem 2 specimens	
Aethiopella handschini (Denis, 1924)	Paclt 1959	Lesotho	D	Mount Morosi, 15 miles NE of Quthing, under stone in wet ravine, alt 6600 ft., 18.3.1951, SSAE leg, loc 241.	4 specimens Museum Lund	Originally described from Addis Ababa, Ethiopia, (Denis 1924)
Aethiopella handschini (Denis, 1924)	Paclt 1959	WC	D	Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.i.1951, loc. 161.	21 specimens Museum Lund. (young specimens only)	Originally described from Addis Ababa, Ethiopia, (Denis 1924)
Anurida maritima Laboulbene, 1865	Lawrence 1953	?	I	No information given.		Cosmopolitan distribution (Fjellberg 1998)
Anurida maritima Laboulbene, 1865	Paclt 1959	WC	I	Strandfontein, False Bay, Nov. 1930, K.H. Barnard leg		Cosmopolitan distribution (Fjellberg 1998)

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Anurida maritima Laboulbene, 1865	Womersley 1934	KZN	I	Durban, Jan 1913 (K.H. Barnard leg).		Cosmopolitan distribution (Fjellberg 1998)
Anurida maritima Laboulbene, 1865	Womersley 1934	WC	I	Saldannha Bay 5.ix.1912, Cape Peninsula 1914, Melkbos Strand 28.x.1927, Kleinmond, Feb 1927, Hout Bay, 11.ii.1914 (all K.H. Barnard leg), Sea Point 31.vii.1930, Muizenberg 26.vii.1930 (Womersley leg).		Cosmopolitan distribution (Fjellberg 1998)
Anurida maritima Laboulbene, 1865	Yosii 1959	WC	I	Seapoint, 30 specimens, 11.iii.1958.	Cosmopolitan distribution (Fjellberg 1998)	Cosmopolitan distribution (Fjellberg 1998)
Ectonura barrai Janion, Bedos & Deharveng, 2011	Janion, Bedos & Deharveng 2011	WC	E	Type locality: Grootvadersbosch Nature Reserve, Heidelberg, 24.viii.2010, Southern Afrotemperate Forest vegetation, in litter, extraction on Berlese funnel, C. Janion leg (RSA10_GVB009, 33°59.167'S, 20°48.639'E).	Holotype and 4 paratypes (1 ♂ and 1 juv on slides, 2 in alcohol) in SAMC; 5 paratypes (1 ♂ and 1 juv on slides, 3 in alcohol) in MNHN	
Ectonura monochaeta Janion, Bedos & Deharveng, 2011	Janion, Bedos & Deharveng 2011	WC	E	Type locality: Cape Town, Table Mountain National Park, 10. iii.2009, native forest, sieving of liter and extraction on Berlese funnel, l. Deharveng & A. Bedos leg, SAF141	Holotype and 6 paratypes on slide (3 ♂, 3 ♀), 25 in alcohol in SAMC; 7 paratypes (3 ♂, 3 ♀ and 1 juv on slides), 25 in alcohol in MNHN	
Ectonura coatesi Barra, 1994	Barra 1994	KZN	E	Sodwana Bay National Park, litter on dunes, 02.ii.1992, J.-P. Rieb leg.	Holotype ♂ and paratype ♀, RMCA, 2 ♀ paratypes with author	
Ectonura natalensis (Womersley, 1934)	Womersley 1934	KZN	E	Inchanga, K.H. Barnard, Nov. 1917	Co-types in SAMC	*Achorutes natalensis* Womersley, 1934
Ectonura natalensis (Womersley, 1934)	Paclt 1959	WC	E	Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.i.1951 loc. 161	1 specimen Museum Lund	*Neanura natalensis* (Womersley, 1934)

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Ectonura natalensis (Womersley, 1934)	Paclt 1959	EC	E	Dordrecht district, small poplar grove from soil containing decomposing leaves (about 18 specimens), October 1957, R. van Pletzen leg.,		*Neanura natalensis* (Womersley, 1934)
Ectonura natalensis (Womersley, 1934)	Paclt1959	KZN	E	Pietermaritzburg, from dry leaves in garden, Sept 1951, 5 specimens, Champagne Castle, Drakensberg, Feb 1946, 1 specimens, R.F. Lawrence leg.		*Neanura natalensis* (Womersley, 1934)
Ectonura oribiensis (Coates, 1968)	Coates 1968	KZN	E	Oribi Gorge, rotting pineapple trash, 2.ii.1966 (T. J. Coates leg) AcV66/114 & 115, 10.xi.1965 and 11.x.1965, virgin soil, Empangeni (G. Nel leg) AcV 65/278 & 287	♂ holotype, two ♀ paratypes, two ♂ paratypes, all in the NIC, Department of Agricultural Technical Services, Pretoria	*Neanura oribiensis* Coates, 1968
Ectonura sp. Cassagnau, 1980	Lawrence 1953	?	?	No information given.		
Ectonura sp. Cassagnau, 1980	Weiner and Najt 1991	WC	?	Saasveld, near George, subtropical indigenous forest, on bark of *Olinia ventosa*, 23.xii.1986, V. Nicolai leg, 1 specimen	1 specimen ISEA	
Friesea claviseta Axelson, 1900	Womersley 1934	KZN	I	Pietermaritzburg, from dry leaves in garden, Sept 1951, R.F. Lawrence, 2 specimens		Cosmopolitan distribution (Fjellberg 1998)
Friesea claviseta Axelson, 1900	Womersley 1934	WC	I	Stellenbosch, 12.xiii.1930, loose damp bark of fallen log (Womersley leg)		Cosmopolitan distribution (Fjellberg 1998)
Friesea versabilis Barra, 1995	Barra 1995	KZN	E	Sodwana Bay, 5 cm depth, under pioneer vegetation, 03.ii.1992, J.-P. Rieb leg.	Holotype female, paratype male, RMCA	
Najtafrica riebi (Barra, 1994)*	Barra 1994	KZN	E	Lake St Lucia, 100km south of Sodwana Bay, foot of first dune, moist sand at 5cm depth under pioneer vegetation, 6.ii.1992, J.-P. Rieb leg.	Holotype ♀ in RMCA, 3 ♀ paratypes (2 juvs) with author	*Stachorutes riebi* Barra, 1994
Neanura muscorum (Templeton, 1835)	Coates 1968a	EC	I	Cathcart C.P. 15.v.1966, pine needle litter, T.J. Coates AcV 66/142.	NIC	Cosmopolitan distribution (Fjellberg 1998)
Pseudachorutella africana	Weiner and Najt	WC	E	Saasveld, near George, subtropical indigenous forest, pitfall	Holotype ♂ (ISEA)	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Weiner and Najt, 1991	1991			traps, 17.xii.1986-17.i.1987, V. Nicolai leg.		
Pseudachorutes alluaudi (Delamare Deboutteville, 1946)	Paclt 1959	KZN	E?	National Park, Gudu Falls, under log in dense indigenous forest, alt about 6000ft, 4.iv.1951, SSAE leg, loc 206, Cathkin Peak, Jan. 1938 R.F. Lawrence leg, 1 specimen, Champagne Castle Hotel, January 1953 R. F. Lawrence leg., 7 specimens, - Ibidem January 1957, R.F. Lawrence leg, 4 specimens.	5 specimens Museum Lund (Gudu Falls)	*Ceratrimeria alluaudi* Delamare Deboutteville, 1946
Pseudachorutes univesicatus Weiner and Najt, 1991	Weiner and Najt 1991	WC	E	Saasveld, near George, subtropical indigenous forest, pitfall traps, 17.xii.1986-17.i.1987, V. Nicolai leg.	Holotype ♀, paratypes 6 ♂, 2 ♀, 4 juv (ISEA), paratypes 4 ♂s, 2 ♀, 5 juv (MNHN)	
Vitronura joanna (Coates, 1968)	Coates 1968a	NWP	E	Potchefstroom, 2.ii.1966, compost, J. Mathew, AcV 66/126. Pretoria, pot plant soil, 15.ix.1966, T. J. coats, AcV 66/157	Holotype ♀, paratype ♂ and 8 ♀, 1 juv paratype, one ♀ paratype (NIC)	*Neanura joanna* Coates, 1968
Vitronura sp. Yosii, 1869	Weiner and Najt 1991	WC	?	Saasveld, near George, subtropical indigenous forest, on bark of *Scolopia mundii* 27.i.1987, V. Nicolai leg.	1 specimen only (ISEA)	
Odontellidae						
Odontella sylvatica Weiner and Najt, 1991	Weiner and Najt 1991	WC	E	Saasveld, near George, subtropical indigenous forest, pitfall traps, 17.xii.1986-17.i.1987, V. Nicolai leg.	Holotype ♀, paratypes 7 (ISEA), 4 paratypes, MNHN	
Odontellina deharvengi Barra, 1995	Barra 1995	KZN	E	St. Lucia, 100km south of Sodwana Bay, 5 cm below pioneer vegetation, 06.ii.1992, J.-P. Rieb leg.	Holotype ♀ and ♂ paratype (RMCA), two paratypes with author	
Superodontella empodialis (Stach, 1934)	Paclt 1959	KZN	?	Champagne Castle, Drakensberg, Feb 1946, R.F. Lawrence leg, 13 specimens		*Odontella empodialis* Stach, 1934 Dubious, described from near Vienna, Austria (Stach 1934)
Onychiuridae						

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Orthonychiurus camerunensis (Schött, 1926)	Paclt 1967	G	I	Krugersdorp, Blyvooruitsig, damp garden soil, 29.ii.1956, 44 specimens AcV88, D.B. Wells leg	NIC	*Onychiurus camerunensis* Schött, 1926
Deuteraphorura inermis (Tullberg, 1869)	Womersley 1934	WC	?	Cape Town, under stones, 3 Aug and 6 Sep 1930 (Womersley leg)		*Onychiurus fimetarius* Tullberg, 1869
Deuteraphorura inermis (Tullberg, 1869)	Re-identified by Paclt 1959	WC	?	Oranjezicht, Cape Town, 4 specimens	SA Museum	*Onychiurus pseudinermis* Tullberg, 1869
Orthonychiurus saasveldensis (Weiner and Najt, 1991)	Weiner and Najt 1991	WC	E	Saasveld, near George, subtropical indigenous forest, on bark of *Scolopia mundii* 27.i.1987, V. Nicolai leg.	Holotype male, paratypes 1 ♀, 1 ♂, (ISEA), paratype 1 ♂ (MNHN)	*Onychiurus saasveldensis* Weiner and Najt, 1991
Protaphorura armata (Tullberg, 1869)	Lawrence 1953	?	I	No information given.		*Onychiurus armata* Tullberg, 1869
Protaphorura matsumotoi (Matsumoto, 1929)	Paclt 1959	FS	?	Bloemfontein, under few pine trees, from soil containing large amounts of organic material, April 1957 (2 specimens), R. van Pletzen leg., Bloemfontein district, garden, from soil containing large amount of organic plant material, August 1957, R. van Pletzen leg, 41 specimens.		*Onychiurus matsumotoi* Matsumoto, 1929
Tullbergiidae						
Delamarephorura szeptyckii Barra & Weiner, 2009	Barra & Weiner 2009	EC	E	Amatola mountains, Hogsback, dry prairie, 1600m a.s.l., August 1995, David Marshall leg.	Holotype ♀ and paratype juvenile MNHN, ♀ paratype ISEA	
Fissuraphorura miscellanea Barra, 1995	Barra 1995	KZN	E	Sodwana Bay, 5 and 20 cm deep pioneer vegetation, 03.ii.1992, J.-P. Rieb leg.	All specimens ♀, holotype and paratype, RMCA	
Tullbergia kilimanjarica (Delamare Deboutteville, 1953)	Paclt 1959	WC	PT?	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 Loc. 79, Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.i.1951, loc. 161all SSAE leg.	1 specimen + 2 Museum Lund	*Mesaphorura kilimanjarica* Delamare Deboutteville, 1953

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Tullbergia kilimanjarica (Delamare Deboutteville, 1953)	Paclt 1959	KZN	PT?	Champagne Castle, Drakensberg, Feb 1946, R.F. Lawrence leg, ,8 specimens, Ibidem, under stones embedded in damp humus in the forest floor, with Eukoenenia and Pauropods, at about 5500 ft., April 1957, R. F. Lawrence leg, 3 specimens, Pietermaritzburg, from dry leaves in garden, Spet 1951, R. F. Lawrence leg. (6 specimens), Bisley, Pietermaritzburg, Oct 1955, R. F. Lawrence leg. (10 specimens)		
Tullbergia kilimanjarica (Delamare Deboutteville, 1953)	Paclt 1967	WC	PT?	van Rhynsdorp, Knersvlakte, 3 miles from van Rhyns pass, 22.iii.1956, 1 specimen AcV93, D.v.V. Webb leg.	NIC	
Tullbergia kilimanjarica (Delamare Deboutteville, 1953)	Coates 1970	MP	PT?	Kruger National Park, under dead leaves, Klopperfontein No. 15		
Mesaphorura krausbaueri (Börner, 1901)	Womersley 1934	WC	?	Hout Bay under stones 4.viii.1930, Cape Town 19.viii.1930, Stellenbosch 18.viii.1930 (Womersley leg)		*Tullbergia krausbaueri* Börner, 1901. Dubious identification, most *Mesaphorura* named *M. krausberi* before slit by Rusek (1971), Old records are not reliable (Fjellberg 1998).
Mesaphorura krausbaueri (Börner, 1901)	Paclt 1959	EC	?	Dordrecht district, small poplar grove from soil containing large amount of decomposed material (about 280 specimens), July and October 1957, R. van Pletzen leg.		*Tullbergia krausbaueri* Börner, 1901. Dubious identification, most *Mesaphorura* named *M. krausberi* before slit by Rusek (1971). Old records are not reliable (Fjellberg 1998).

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Mesaphorura krausbaueri (Börner, 1901)	Paclt 1959	FS	?	Bloemfontein, garden, from soil containing large amount of organic plant material, August 1957, R. van Pletzen (about 250 specimens)		*Tullbergia krausbaueri* Börner, 1901. Dubious identification, most *Mesaphorura* named *M. krausberi* before slit by Rusek (1971). Old records are not reliable (Fjellberg 1998).
Mesaphorura yosii (Rusek, 1967)	Barra 1995	KZN	I	Sodwana Bay		
Paratullbergia callipygos (Börner, 1902)	Womersley 1934	WC	I	Cape Town, August 1930 (Womersley leg)		*Tullbergia callipygos* Börner, 1902. Dubious: general distribution described as Holarctic (Fjellberg 1998).
Tullbergia meridionalis Cassagnau & Rapoport, 1962	Barra 1995	KZN	PT?	St. Lucia, 100km south of Sodwana Bay, wet sand at foot of dune, 06.ii.1992, J.-P. Rieb leg.		
ENTOMOBRYOMORPHA						
Cyphoderidae						All species from this family not described from SA should be taken with caution, as this genus needs revision.
Calobatinus rhadinopus (Börner, 1913)	Börner 1913	KZN	E	4 specimens (3 ♀, 1♂), nest of *Macrotermes natalensis*, 23.vi.1898, no specific location given, Dr. J. Trägardhs leg.		*Calobatella rhadinopus* Börner 1913
Calobatinus rhadinopus (Börner, 1913)	Paclt 1967	G	E	10 miles East of Pretoria, shelving and fungus comb in nest of *Macrotermes natalensis,* 25.ii.1963, 3 males and 5	NIC	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				females T.23; Rust de Winter, Farm Rooikop, fungus comb in nest of *M. waterbergi* 13.iii.1963, 13 females T.38, all J.S. Sheasby leg.		
Cyphoderus cf. assimilis Börner, 1906	Paclt 1967	KZN	?	Van Rhynsdorp, top of van Rhyns pass, 26 miles from van Rhynsdorp, under stones, 22.iii.1956, 2 specimens, AcV95, D.v.V. Webb leg.	NIC	Paclt (1967) noted these specimens immature and damaged.
Cyphoderus assimilis Börner, 1906	Paclt 1959	KZN	PT?	Albert Falls, in ants' nests, May 1942, R.F. Lawrence leg. (7 specimens)		
Cyphoderus bidenticulatus Parona, 1888	Börner 1913	KZN	E?	Nest of *Odontotermes latericius*		
Cyphoda colurus (Börner, 1908)	Börner 1908	NC	?	Steinkopf, nest of termite *Hodotermes viator,* July 1904, 3 specimens, L. Schultze leg.		*Cyphoderus colurus* Börner, 1908. Dubious: Paclt (1959) noted that this species has not been rediscovered since original description.
Cyphoda limboxiphia (Börner, 1913)	Börner 1913	KZN	PT?	Nest of termite *Trinervitermes trinervius*		*Cyphoderus limboxiphius* Börner, 1913
Cyphoda limboxiphia (Börner, 1913)	Paclt 1967	G	PT?	3.6 miles from Pretoria on Warmbaths Road, shelving and fungus comb in cabity of *Odontotermes transvaalensis,* 11.ii.1963, 1 specimen T.2, 4 specimens t.4, 18.ii.1963, 1 specimen t.14 and 8.iii.193, 56 specimens T.34; Rust de Winter, Farm Rooikop, fungus comb in nest of *O. badius,* 19.iii.1963, 12 specimens T.50, all material J.L. Sheasby leg.		
Cyphoda natalensis (Börner, 1913)	Börner 1913	KZN	E	Nest of termite *Macrotermes natalensis*		*Cyphoderus natalensis* Börner, 1913
Cyphoda natalensis (Börner, 1913)	Womersley 1934	WC	E	Ants' nests, Table Mountain, Cape Town, 27 July 1930, Hout Bay Aug 1930 (Womersley leg).	Two of these specimens observed by Paclt 1959 in SAMC	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Cyphoderus omoensis Delamare Deboutteville, 1945	Paclt 1959,	WC	Africa?	On stalagmites (according to slide) Cango Caves, Oudtshoorn, Nov. 1929, K.H. Barnard leg.		Slide from SAMC examined and re-identified by Paclt, specimen incorrectly identified as *Cyphoderus arcuatus* var. *aethiopicus*
Cyphoderus squamidives Silvestri, 1918	Paclt 1959	KZN	Africa	Champagne Castle, Drakensberg, Feb 1946, R. F. Lawrence leg (2 specimens)		
Cyphoderus squamidives Silvestri, 1918	Paclt 1967	WC	Africa	Simons Town, Termite Research Laboratory of the Division of Entomology, Simons Town, soil in colony of *Coptotermes formosanus* 9.viii.1956, 69 specimens, AcV107, Mrs P.E. de Wet leg.	NIC	
Cyphoderus squamidives Silvestri, 1918	Silverstri 1918	G	Africa	Pretoria, together with *Calobatinus rhadinopus*, with termites *Macrotermes natalensis.*		
Cyphoderus trinervoidis Paclt, 1965	Paclt 1965	G	Africa	18 miles from Pretoria in the direction towards Babsfontein, in nest of *Trinervitermes trinervoides* (Sjöstedt), J. L. Sheasby leg. 27.ii.1963	Holotype SMF A 1677 and 14 paratypes SMF A 1678, 17 paratypes in Entomol. Avdeln. Zool. Inst. Univ. Lund, 12 paratypes in NIC, Locality T.27	
Pseudocyphoderus wasmanni Börner, 1913	Börner, 1913	KZN	E	Nests of termite *Odontotermes vulgaris*, November 1898, no specific location given.		
Pseudocyphoderus wasmanni Börner, 1913	Paclt 1967	G	E	35.6 miles from Pretoria on the Warmbaths road, shelving and fungus comb in nest of *Odototermes transvaalensis* 11.ii. 1963, 6 specimens T.4; Waverley, 7 miles east of Pretoria, shelving and fungus comb of *O. latericius*, 20,ii.1963, 11 specimens T.21; near Vlakfontein 10 miles east of Pretoria, shelving and fungus comb of *Macrotermes natalenis*, 25.ii.1963, 46 specimens T. 23, all J.S. Sheasby leg.		
Entomobryidae						

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Capbrya marshalli Barra, 1999*	Barra 1999	EC	E	Hogsback, Amatola Mountains, 1600m a.s.l. in Themeda grassland, 40 km from University of Alice	Holotype ♀ and three paratypes ISNB	
Capbrya themeda Barra, 1999*	Barra 1999	EC	E	Hogsback, Amatola Mountains, 1600m a.s.l. in Themeda grassland, 40 km from University of Alice	Holotype female and two paratypes ISNB	
Entomobrya atrocincta Schött, 1897	Paclt 1967	WC	I	Paarl, fallen leaves, 29.viii.1956, 7 specimens AcV29, D.v.V. Webb leg	NIC	
Entomobrya cf. *nivalis* Linnaeus, 1758	Yosii 1959	WC	?	Kloof nek, 5.xii.1957, 4 specimens	♀ of young stage, exact identification is not possible	
Entomobrya decemfasciata (Packard, 1873)	Womersley 1934	WC	?	Muizenberg 25 July 1930 Womersley leg.		Dubious, although not recorded in Europe (Jordana, 2012)
Entomobrya hexfasciata Harvey, 1896	Paclt 1959	FS	?	Bloemfontein District, in garden, from soil containing large amounts of plant material, Aug 1957, R. van Pletzen leg, (1 specimen)		Dubious, although not recorded in Europe (Jordana, 2012)
Entomobrya hexfasciata Harvey, 1896	Paclt 1959	G		Johannesburg, Ventersdorp Gold Mine, in decaying timber, June 1943, Miss. D. Weintroub leg. (32 specimens).		Dubious, although not recorded in Europe (Jordana, 2012)
Entomobrya minima Brown, 1926	Brown 1926	KZN	E	Umkomaas, under a stone, 16.vii.1917, P.A. Boxton leg.	not mentioned	Dubious, although not recorded in Europe (Jordana, 2012)
Entomobrya multifasciata (Tullberg, 1871)	Paclt 1967	WC	I	Paarl, fallen leaves, 29.viii.1947, 20 specimens AcV29; Mamre Roadm Waterkloof Farm, July 1937, 2 specimens AcV30, all D.v.V. Webb leg	NIC	
Entomobrya multifasciata (Tullberg, 1871)	Paclt 1967	NC	I	Upington, banks of Orange River, Dec 1937, 3 specimens, AcV48, D.v.V. Webb leg	NIC	
Entomobrya multifasciata (Tullberg, 1871)	Paclt 1967	G	I	Pretoria, Parktown, grass on banks of Apies River, 24.ix.1937, 2 specimens, AcV45 D.v.V. Webb leg	NIC	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Entomobrya nivalis (Linnaeus, 1758)	Coates 1970	WC	I	Tsitsikama Forest and Coastal NP, from rotting leaves in indigenous forest, Storms River		
Entomobrya nivalis (Linnaeus, 1758) f. *immaculata* (Schäffer, 1896)	Womersley 1934	WC	I	Rondebosch, Cape Town, 29.vii.1930 Womersley leg.		
Entomobrya nivalis Linnaeus, 1758 f. *maculata* Schäffer, 1896	Womersley 1934	WC	I	Stellenbosch, 28.viii.1927 Dr. Hesse leg., Rondebosch, Cape Town, 29.vii.1930 Womersley leg.		
Entomobrya nivalis (Linnaeus, 1758)	Paclt 1959	WC	I	Tsitsikama Forest, Storms river, 12.i.1951, SSAE leg, loc. 134 (5 specimens), Cape Peninsula, Cape Point Nature Reserve, sieved from wet sieved on low bush, 10.xii.1950, SSAE leg., loc. 79 (3 specimens), Groot Swartberg Mountain Range, Cango caves, 19.x.1948 (2 specimens), B. Hanstrom leg.	Museum Lund	
Entomobrya nivalis (Linnaeus, 1758)	Paclt 1959	EC	I	Dordrecht district, from heap of decomposing mealie cobs (21 specimens), July and October 1957, R. van Pletzen leg. (1 specimen)		
Entomobrya nivalis (Linnaeus, 1758)	Paclt 1959	FS	I	Fouriesburg District, from surface of rainwater pool, January or April 1957, R. van Pletzen leg. (1 specimen)		
Entomobrya nivalis (Linnaeus, 1758)	Paclt 1967	KZN	I	New Hanover, Ashenden Estates, on exterior of the wattle bagworm *Kotochalia junodi,* 21.viii.1947, 1 specimen AcV85, D.v.V. Webb leg.	NIC	
Entomobrya sp. Rondani, 1861	Paclt 1967	WC	?	Gordons Bay, grass near sea, 4.viii.1937, 6 specimens, AcV32, Somerset West, 4.viii.1937, 1 specimen AcV33; Gordons bay, 10.viii.1937, 1 specimen, AcV38, all D.v.V. Webb leg.	NIC	
Entomobrya sp. Rondani, 1861	Lawrence 1953	?	?	No information given		
Entomobrya sp. *(cf. nivalis)* (Linnaeus, 1758)	Yosii 1959	WC	?	Kloof Nek, 4 specimens, 5.xii.1957, all young females		
Lepidocyrtinus incertus (Handschin, 1926)	Womersley 1934	WC	?	Keurbooms Estuary, Jan. 1916 (K.H. Barnard leg)		Dubious
Lepidocyrtinus pseudocoeruleus Denis, 1924	Womersley 1934	WC	?	Franch Hoek 2000 feet Dec 1916 (K.H. Barnard leg.), Kirstenbosch 23.vii.1930, Hout Bay August 1930, Signal Hill, Cape Town, 31.viii.1930 (all Womersley leg.)		

Current species name	**Source**	**SA**	**Status**	**Records**	**Collection**	**Comments / Reference**
Lepidocyrtus cf. lanuginosus (Gmelin, 1788)	Yosii 1959	WC	I	Table Mountain, 10 specimens, 5.xii.1957		*Lepidocyrtus cf. lanuginosus* (Gmelin, 1788)
Lepidocyrtus cf. *lanuginosus* (Gmelin, 1788)	Paclt 1967	WC	I	Mamre Road, Waterkloof Farm, 3.vi.1937, 3 specimens AcV28; Gordons Bay, 4.viii.1937, 2 specimens AcV34, 11.viii.1937, 2 specimens, AcV40 and 5.vii.1938, 7 specimens AcV55; Velddrift, damp soil along banks of berg River, 20.iii.1956, 1 specimenAcV90; Hout Bay Chapmans Peak Drive, damp soil and moss, 22.iv.1956, 1 specimen AcV102, all D.v.V. Webb leg.	NIC	*Lepidocyrtus* cf. *lanuginosus* (Gmelin, 1788)
Lepidocyrtus cyaneus Tullberg, 1871	Paclt 1959	KZN	I	Pietermaritzburg, dry leaves in garden, R.F. Lawrence leg., Sept 1951 (1 specimen), Drakensberg, about 13 miles ENE from Rhodes, among stones on mountain slope, at small stream, 8000 ft., 9.iii.1951, SSAE leg, Loc. 219	1 specimens Museum Lund (SSAE leg)	
Lepidocyrtus cyaneus Tullberg, 1871	Paclt 1959	EC	I	Dordrecht district, small poplar grove from soil containing large amount of decomposed material (2 specimens), October 1957, R. van Pletzen leg.		
Lepidocyrtus ferrugineus (Schött, 1893)	Paclt 1959	KZN	Africa	Pietermaritzburg, dry leaves in garden, R.F. Lawrence leg., Sept 1951 (120 specimens)		
Lepidocyrtus lanuginosus (Gmelin, 1788)	Paclt 1967	WC	I?	Table Mountain Drive, humus and pine needles, 5.v.1956, 7 specimens, AcV105, D.v.V. Webb leg	NIC	
Lepidocyrtus lanuginosus (Gmelin, 1788)	Womersley 1934	WC	I?	Franschhoek 200 feet, Dec. 1926 (K.H. Barnard leg), Stellenbosch 12.viii.1930, Rondebosch 19.vii.1930, Cape Town 24.viii.1930, Signal Hill 31.viii.1930, Hout Bay 30.viii.1930, Kirstenbosch 2.viii.1930 (all Womersley leg.)		
Lepidocyrtus sp. Bourlet, C, 1839:391	Lawrence 1953	?	?	No information given.		
Lepidokrugeria meyerae Coates, 1969*	Coates 1969	MP	E	Letaba River, Kruger National Park, N237, TvL., dead leaves, 14.i.1964, T. J. Coates AcV64/94 and under *Protulacaria afra*, Shingwidzi Rest Camp (CATES 1970)	Holotype, 3 paratypes from KNP, PPRI Pretoria?, not listed, 30 other specimens from KNP, Groblersdal	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					and Machava, Mozambique.	
Pseudosinella alba (Packard, 1873)	Paclt 1959	WC	?	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 SSAE leg. Loc. 79	8 specimens Museum Lund	
Pseudosinella alba (Packard, 1873)	Paclt 1959	EC	?	Dordrecht district, from heap of decomposing mealie cobs (7 specimens), July and October 1957, R. van Pletzen leg., also small poplar grove from soil containing decomposing leaves (21 specimens)		
Pseudosinella biguttata Barra 1997	Barra 1997	KZN	E	Superficial litter and humus on dunes, sandy forest bush shrub, 02.ii.1992, J.-P. Rieb leg.	Holotype ♀, one paratype and one other example, MNHN	
Pseudosinella cf. *candida* Folsom, 1902	Yosii 1959	WC	I	Kloof Nek, 5.xii.1957, 31 specimens		
Pseudosinella immaculata (Lie-Pettersen, 1897)	Paclt 1959	KZN	?	Champagne Castle, Drakensberg, Feb 1946, R.F. Lawrence leg. (7 specimens)		
Pseudosinella octopunctata Börner, 1901	Paclt 1959	WC	I	Table Mountain, Wynberg Cave Ravine, sieved from wet vegetable debris, alt 2400ft, 18.xii.1950, SSAE leg. Loc. 84	6 specimens Museum Lund	
Pseudosinella octopunctata Börner, 1901	Paclt 1959	FS	I	Bloemfontein, under few pine trees, from soil containing large amounts of organic material, April 1957 (1 specimen)		
Seira addoensis Coates, 1968	Coates 1968	EC	E	Holotype from under grass, Addo Elephant NP, 12.i.1965 AcV65/98; 2 paratypes one from soil andother one from *Euclea undulata* Addo Elephant NP, 11.i.1965 AcV65/46 & 47. Several other specimens, but with incomplete antennae, all T.J. Coates leg.	Holotype and 2 paratypes, NIC	
Seira anncla Coates, 1968	Coates 1968	EC	E	Grahamstown district; holotype and 1 paratype from *Scutia myrtina* (Burm. F) Kurz and 4 paratypes from Gewsia sp, 13.i.1965, T.J. Coates leg, AcV65/67, 69, 70. About 40 other specimens from the Eastern Cape.	Holotype and 5 paratypes, NIC	
Seira anncla Coates, 1968	Coates 1970	WC	E	Tsitsikama Forest and Coastal NP, on grass next to sea, Mountain Zebra NP, on unidentified shrub.		
Seira annulicornis (Börner, 1903)	Yosii 1959	WC	PT	Table Mountain, 8 specimens, 11.iii.1958		*Lepidocyrtinus annulicornis* Börner, 1903

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Seira annulicornis (Börner, 1903)	Coates 1970	MP	PT	Kruger National Park, Klopperfontein, in soil around pool.		
Seira annulicornis (Börner, 1903)	Coates 1968	G	PT	Wide distribution		
Seira annulicornis (Börner, 1903)	Coates 1968	FS	PT	Wide distribution		
Seira annulicornis (Börner, 1903)	Coates 1968	KZN	PT	From north-east of a line joining Pongola and Pretoria, incl. Mozambique, about 250 specimens.		
Seira annulipes (Handschin, 1929)	Womersley 1934	KZN	PT	Inchanga, Nov 1917 (K.H. Barnard leg)	24 specimens in SAM (according to Coates 1968)	*Lepidocyrtus annulipes* Handschin, 1929
Seira annulipes Handschin, 1929	Womersley 1934	WC	PT	Keeromberg, Worcester Mountains, 3500 feet, Sept 1930 (K.H. Barnard leg)		
Seira barnardi (Womersley, 1934)	Coates 1970	WC	E	Tsitsikamma Forest and Coastal NP, on *Passerina* sp.		*Lepidocyrtinus cooperi* var. *barnardi* Womersley, 1934
Seira barnardi Womersley, 1934	Yossi 1959	WC	E	Cape Town, Kirstenbosch, 47 specimens, 10.iii.1938 (1958?)		
Seira barnardi Womersley, 1934	Paclt 1967	NWP	E	Marico District, fallen leaves, 13.i.1930, one specimen AcV3, J.C. Faure leg	NIC	
Seira barnardi Womersley, 1934	Paclt 1967	WC	E	Port St. Johns, 14.i.1931, 4 specimens, AcV4, W. Powell leg	NIC	
Seira barnardi Womersley, 1934	Womersley 1934	WC	E	Cape Town 16.xii.1916, 1.viii.1915 1000 feet (K.H. Barnard leg), Kirstenbosch 22.vii.1930 (Womersley leg)	Co-types in SAM (slide 73, 75 and 76).	
Seira barnardi Womersley, 1934	Coates 1968	WC	E	Suurbraak, Swellendam and Tsitsikama District (T.J. Coates leg)		
Seira barnardi Womersley, 1934	Paclt 1959	WC	E	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950, loc. 79 (12 specimens), Table Mountain, Wynberg Cave Ravine, sieved from wet debris, 2400ft, 18.xii.1950 loc 84 (32 specimens), Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600ft, 28.i.1951, loc.161 (15 specimens),	Museum Lund	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				all SSAE leg.		
Seira capensis (Womersley, 1934)	Womersley 1934	WC	E	Type locality: Matroosberg 3500 feet Jan 1917 (Ceres side, Farm Laken Vallei, K.H. Barnard leg)	Co-types in SAMC (slide 82 and 83 according to Coates 1968)	*Lepidocyrtinus capensis* Womersley, 1934
Seira capensis (Womersley, 1934)	Yosii 1959	WC	E	♀ specimen from Porcupine Buttress 11.iii.1958, male from Kloofnek 6.xii.1957		
Seira capensis (Womersley, 1934)	Coates 1968	WC	E	Citrusdal and Tulbagh (T.J. Coates leg), 166-167.		
Seira capensis (Womersley, 1934)	Coates 1968	EC	E	Port Alfred (T.J. Coates leg), 166-167.		
Seira damerella Coates, 1968	Coates 1968	L	E	Holotype and 1 paratype from grass under citrus, Politsi, 16.i.1964, 1 paratype from under dead leaves at Letsitele, 1 from grass at Phalaborwa, both 16.i.1964, about 20 specimens from Lowveld, all T.J. Coates leg.		
Seira damerella Coates, 1968	Coates 1970	MP	E	Kruger National Park, under dead leaves, Letaba River, No. 237 and under *Hyphaene crinita*, Shingwidzi Rest Camp.		
Seira damerella Coates, 1968		MP	E	One paratype from mulch in banana orchard, Nelspruit, 7.vii.1966, T.J. Coates leg.		
Seira dayi Yosii, 1959	Yosii 1959	WC	E	Skeleton Gorge, 3 specimens, 6.xii.1957		
Seira dayi Yosii, 1959	Coates 1968	WC	E	10 specimens from Grootvadersbosch and Heidelberg, T.J. Coates leg		
Seira eleana Coates, 1968	Coates 1968	MP	PT	Kruger National Park, under dead leaves, No. 41; under rotting leaves, Shingwidzi Rest Camp; from soil, Klopperfontein; under elephant droppings, Shingwidzi Rest Camp, under dead leaves, Letaba River, No 237 and also no. 216.		Also recorded from Yemen by Barra (2004)
Seira eleana Coates, 1968	Coates 1968	MP	PT	Holotype and 4 paratypes from dry grass, Bundu Inn Groblersdal district, 15.iii.1967, AcV 67/14. About 100 other specimens from the Kruger NP and Mozambique.	NIC	
Seira flavovirens (Börner, 1903)	Womersley 1934	WC	PT	Fransch hoek 200 feet Dec1916, Matroosberg Ceres side, Farm Laken Vallei 3500 feet Jan 1917 (K.H. Barnard leg), Hout Bay Aug 1930 (Womersley leg)	2 specimens in SAMC according to Coates (1968)	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Seira flavovirens (Börner, 1903)	Coates 1968	WC	PT	Elsenberg, Trawal		
Seira flavovirens (Börner, 1903)	Yosii 1959	WC	PT	Porcupine Buttress, 2 specimens, 8.iii.1958		
Seira flavovirens var. *annulosa* Wahlgren, 1906	Womersley 1934	WC	E	Muizenberg , shore herbage, 25.vii.1930 (Womersley leg)		
Seira grisea var *annulata* Womersley, 1934	Womersley 1934	WC	E	Kirstenbosch, 23.vii.1930 Womersley leg.	Co-types in SAMC	
Seira grisea (Womersley, 1934)	Womersley 1934	WC	E	Rosebank, Cape Town 22.vii.1930, Kirstenbosch 23.vii.1930 Womersley leg.	Lectotype and paralectotype SAM, re-description by Coates 1968 based on slide 71 (remounted)	*Pseudosira grisea* Womersley, 1934
Seira grisea Womersley, 1934	Coates 1968	WC	E	2 specimens from *Hedera helix,* Katberg, 15.i.1965, AcV65/74, and 2 specimens from *Elytropappus rhinocerotis* Bontebok National Park, Swellendam, 7.ii.1967, AcV 66/167, all T.J. Coates leg.	NIC	
Seira lindei Coates, 1968	Coates 1968	EC	E	Type locality: Holotype and 2 paratypes from rotting leaves in stream, Mountain Zebra NP, 29.i.1965 AcV65/28; 2 paratypes from rotting grass, Zuurberg, 13.i.1965 AcV65/65; other specimens from Addo, Fort Beaufort, van Stadens River, and , all T.J. Coates leg.	NIC	
Seira lindei Coates, 1968	Coates 1968	WC	E	Heidelberg, Piekenierskloof, T.J. Coates leg.		
Seira marephila Coates, 1968	Coates 1968	WC	E	Type locality: Holotype from *Zygophyllum* sp.Hartenbos, 25.i.1965 AcV65/32; 2 paratypes from rotting leaves, Storms River Mouth, 20.i.1965, 3 paratypes from *Rhus undulata, Serruria fucifolia* and under rotting wood respectively, Bontebok NP, 7 and 8.ii.1967 AcV66/169, 171 and 172. 30 other specimens from coast between East London and Mossel Bay, all T.J. Coates leg.	NIC	
Seira marephila Coates, 1968	Coates 1968	EC	E	30 other specimens from coast between East London and Mossel Bay, all T.J. Coates leg.		
Seira mathewsi Coates, 1968	Coates 1968	EC	E	1 paratype from Grewia sp, Mountain Zebra National Park,	3 paratypes, NIC	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				27.i.1965, AcV65/37, 2 paratypes fom grass in vlei, Joubertina, 16.i.1965, AcV65/36 (all T.J.Coates leg).		
Seira mathewsi Coates, 1968	Coates 1968	WC	E	Type locality: Holotype from *Serruria fucifolia* and 3 paratypes from *Chondropetalum nudum* Bontebok National Park, Swellendam, 8.ii.1967, AcV67/172 & 173, other specimens from Grootvadersbosch (all T.J.Coates leg).	Holotype, NIC	
Seira metala Coates, 1968	Coates 1968	WC	E	Type locality: Grootvadersbosch, Swellendam District, holotype and 2 paratypes from under decaying bluegum leaves, 9.ii.1967 T.J. Coates leg, AcV66/182	Holotype and 2 paratypes, NIC	
Seira metarsiosa Coates, 1968	Coates 1968	FS	E	Type locality: Holotype and 3 paratypes from grass, Hammonia district, 16.viii.1967, T.J. Coates leg, AcV67/49, about 65 other specimens from Edenville, Fiscksburg and Clocolan.	Holotype and 3 paratypes	
Seira metarsiosa Coates, 1968		NC	E	2 paratypes from lucerne, Kakamas, 2, Dec 1965, M.K.P. Meyer leg AcV65/274	2 paratypes, NIC	
Seira metarsiosa Coates, 1968		NC	E	Groblersdal.		
Seira munroi Paclt, 1959	Pactl 1959	NC	E	Type locality: Kalahari Gemsbok National Park, Tweede Rivieren, in ants' nests, 12-20.2.1958, H.K. Munro leg.	1 holotype and 24 paratypes Dept. Agric Pretoria, 7 paratypes Museum Lund, 20 paratypes in author's collection	
Seira nagatai Yosii, 1959	Yosii 1959	WC	E	Type locality: Kloof Nek (2 specimens) 9.xii.1957, Kirstenbosh (2 specimens) 8.xii.1957, Skeleton Gorge (10 specimens) 10.iii.1958.		
Seira nyassica (Börner, 1908)	Börner 1908	NC	E	Steinkopf, Little Namaland, Spring 1904, 20 young and adult specimens, L. Schultze leg.		*Pseudosira nyassica* var. *pallens* Börner 1908
Seira pseudocoerulea Denis, 1924	Yosii 1959	WC	PT	Skeleton Gorge, 5 specimens, 11.iii.1958.	.	
Seira rowani (Yosii, 1959)	Yosii 1959	WC	E	Top of Table Mountain, 18 specimens, 11.iii.1958.		*Afroseira rowani* Yossi, 1959
Seira rowani (Yosii, 1959)	Coates 1970	WC	E	Tsitsikama Forest and Coastal National Park, on *Passerina*		

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				sp and on unidentified shrub, Storms River Mouth.		
Seira rowani (Yosii, 1959)	Coates 1968	WC	E	Tsitsikama National park, T.J. Coates leg., 4 specimens.		
Seira rykei Coates, 1968	Coates 1968	WC	E	Holotype and 1 paratype from *Metalasia muricata* Less., Robinson Pass, 25.i.1965, AcV65/16; 2 specimens from *Helichrysum crispum* Less., Grootvadersbosch and one from grass, Suurbraak, 11.ii.1965, AcV66/187 & 189 (all T.J.Coates leg).	NIC	
Seira squamoornata (Scherbakov, 1898)	Paclt 1959	WC	?	Yzerfontein, under succulents on sandy beach (fig. 25), 25.x.1950, SSAE leg., loc. 17 (1 specimen). - Franschhoek Bosreserve: Upper Berg River at the stream, alt. 1500 ft., 1.xi. 1950, SSAE leg., loc. 21 (1 specimen) - Cape Peninsula, Cape Point, Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950, SSAE leg., loc. 79 (2 specimens). – Cape Peninsula, Hout Bay, Skoorsteenkop, in insect trap, ~22.xii1950, loc. 78 (I specimen) - 7 miles SW of Bredasdorp in shallow cave in limestone hill about 2 yards from the opening of the cave, 30.xii.19, SSAE leg., loc. 99 (1 specimen) - Ibidem, under stones and among vegetable debris on limestone hill, covered by bush, 30.xii.1950, SSAE leg., loc. 99 (I specimen) - Addo, in garden, 5.i.1951, SSAE leg., loc. a2 (1 specimen) - Cape Peninsula, Hout Bay. Skoorsteenkop, in insect trap, alt. 650 ft., 22-28.i. 1951, SSAE leg. cf. loc. 157 (12 specimens) – Ibidem, sieved from vegetable debris in dense indigenous forest, alt. 600 ft., 28.i. I951, SSAE leg., loc. 161 (1 specimen).	All specimens Museum Lund	Not considered to occur in SA.
Seira squamoornata (Scherbakov, 1898)	Paclt 1959	KZN	?	Howick Falls, 9.iii.1905, I. TRAGARDH leg (1 specimen) National Park, Tugela Valley, under stone on fairly wet meadow, alt. about 5000 ft., 3.iv.1951. SSAE leg., loc. 258 (1 specimen) -Albert Falls, in ants' nests, May 1942, R. F. LAWRENCE leg. (1 specimen). - Champagne Castle in the Drakensbergen, February 1946, R. F. Lawrence leg. (25 specimens). – Mont-aux-Sources in the Drakensbergen, alt. 10,500 ft., March 1946, R. F. Lawrence leg. (5 specimens). - Pietermaritzburg, from dry leaves in garden, September	Museum Lund	Not considered to occur in SA.

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				1951, R. F. LAWRENCE leg. (2 specimens). - Champagne Castle in the Drakensbergen, Hotel, January 1951, R. F. Lawrence leg. (4+11 specimens). - Basutoland: Makheke Mountains, 15 miles ENE of Mokhotlong, at stony stream in alpine mountain valley, alt. 9500 ft., 7.iv.1951, SSAE leg, loc. 268 (1 specimen), Hluhluwe Game Reserve, swept among grass, 17.iv.1951, SSAE leg., loc. 276 (1 specimen).		
Seira squamoornata (Scherbakov, 1898)	Paclt 1959	FS	?	Bloemfontein, under a few pine trees, from soil containing large amount of organic plant material, especially fallen needles of pine trees, April 1957, R. VAN PLETZEN leg. (2 specimens).		Not considered to occur in SA.
Seira squamoornata (Scherbakov, 1898)	Paclt 1959	G	?	Northen Transvaal, Forst Entabeni, Zoutpansberg Mountains (etwa 40 km ostl. Louis Trichardt). ca. 1500 m, aus Fall-Laub von verschiedenen durcheinander wachsenden Bauman mittels Trichter-Falle im Labor. in Pretoria gcwonnen. Mai 1957 (108)", R. STRASSEN leg. (1 specimen, SMF 1381').		Not considered to occur in SA.
Seira squamoornata (Scherbakov, 1898)	Paclt 1967	WC	?	Gordons Bay, Steenbras River mouth, moss and rotten leaves, I.viii.1937, 5 specimens AcV31; Gordons Bay, grass near sea, 4.viii.1937, 2 specimens AcV32; Somerset West, 4.viii.1937, three specimens AcV33; Gordons Bay, 4.viii.1937, 12 specimens AcV34 and 9.viii.1937, 5 specimens AcV35; Strand, 02.viii.1937, 16 specimens AcV39; GordonsBay, 02.viii.l937, 17 specimens AcV40; Somerset West, Sir Lowrys Pass, 12.viii.1937, 7 specimens AcV41; Gordons Bay, 13.VIII.1937, 10 specimens AcV42; Palmiet River, near Kleinmond, 17.viii .193 7, 17 specimens AcV44 ; Gordons Bay, 5.viii.1938, 8 specimens AcV55; Velddrift, damp soil on banks of Berg River 20.iii.1956, 2 specimens AcV90; Langebaan,Oesterwal, grass sweepings along lagoon, 20.iii.1956, 19 specimens AcV91; Citrusdal, banks of Olifants River 15 miles on Clanwilliam road, 21.iii.1956, three specimens AcV92; Clanwilliam, 8 miles on van Rhynsdorp road, 22.iii.l956, three specimens AcV94;	NIC	Not considered to occur in SA.

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				Baineskloof Pass, along mountain stream 7 miles from Wellington, 23.iii.1956, 6 specimens AcV96; Calvinia, 120 miles on Ceres road, 23.iii.1956, 6 specimens AcV97; Muizenberg, Boyes Drive Waterfall, damp soil and moss, 15.iv.1956, 2 specimens AcV98; all material D.v.V. Webb leg.		
Seira squamoornata (Scherbakov, 1898)	Paclt 1967	NC	?	Keimoes, banks of Orange River, December 1937, one specimen AcV46 and 21 specimens AcV50; Upington, banks of Orange River, December 1937, 9 specimens AcV47, 13 specimens AcV48, 8 specimens AcV49, 13 specimens AcV51 and 5 specimens AcV53; Steytlerville, banks of Sundays River, 5.x.1938, 10 specimens AcV56; Uitenhage, Prickly Pear Laboratory, 17.x.1938, 6 specimens AcV57 and Gubb Location, 17.x.1938, 8 specimens AcV58; Glenconner, 28.x.1938, 3 specimens AcV59; Uitenhage, Prickly Laboratory, 2.xi.1938, 7 specimens AcV60, 3.xi.l938, 18 specimens AcV61 and in Wardian cases containing rotted *Opuntia* pads, 4.iv.1939, 16 specimens AcV62; Aberdeen, 2 I.ix. 1939, 14 specimens AcV69; Graaff-Reinet 23.ix.1939, 12 specimens AcV70, 25.ix.1939, 3 specimens AcV72 and 29.ix.1939, 13 specimens AcV73.	NIC	Not considered to occur in SA.
Seira squamoornata (Scherbakov, 1898)	Paclt 1967	KZN	?	Nongoma, grass sweepings, 15.ix.l922, 28 specimens AcV1; Ingwavuma, grass sweepings, 18.ix.1922, 51 specimens AcV2; all material J. C. Faure leg.; Cedara 11-26.xii.1937, 86 specimens AcV54; Estcourt District, Upper Luteni River, altitude of ± 5000 ft at foot of main Drakensberg mountain range, July 1941, 13 specimens AcV74, 11 specimens AcV75,. 18 specimens AcV76, II specimens AcV77 and II specimens AcV78; Estcourt District, Cathkin Peak, Champagne Castle Hostel, at altitude of ± 6000 ft on slopes of main Drakensberg mountain range, July 1942, 17 specimens AcV79; Mkuzi Game Reserve, grass sweepings, 2I.x.1945, 17 specimens AcV80, light traps, December 1945-January 1946, 5 + 160 specimens AcV81, 1650 specimens;	NIC	Not considered to occur in SA.

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				AcV82, and May 1947,176 specimens AcV83; Idem, Umboneni Pan, damp soil, 25.v.1947, 62 specimens AcV84 and Uyenya Pan, 21.ix.1947, six specimens AcV86; Mtubatuba, Duku Duku Forest, 23.ix.1947, 7 specimens AcV87; all material D.v.V. Webb leg.		
Seira squamoornata (Scherbakov, 1898)	Paclt 1967	G	?	Pretoria, Parktown, grass on banks of Apies River, 24.ix.1937, 1 specimen AcV45, D.v.V. Webb; Rust de Winter, Farm Rooikop, in fungus comb of nest of *Odontotermes transvaalensis* (Sjbst), 20.vi.1963, one specimen T.I07, J. L. Sheasby.	NIC	Not considered to occur in SA.
Seira laeta (Börner, 1908)	Börner 1908	NC	E	Port Nolloth, April 1905, 3 specimens, L. Schultze leg.		*Pseudosira laeta* Börner, 1908
Seira tsikama Coates, 1968	Coates 1968	WC	E	Holotype under oak leaves, Tsitsikama Seacoast National Park, 19.i.1967 (T.J. Coates leg), AcV65/96; paratype from rotting leaves Storms River Mouth, 20.i.1967 T.J. Coates leg) AcV65/104; 1 paratype from indigenous forest litter, Knysna, 9.iv.1966 (J. Findlay leg) aVc66/136.	Holotype and 2 paratypes, NIC	
Seira vaneedeni Coates, 1968	Coates 1968	KZN	E	Holotype from grass, Oribi Gorge, 2.ii.1966 AcV66/116; 1 paratype from unidentified shrub, Charters Creek, St. lucia, 24.i.1966 AcV66/63; 3 paratypes from grass, Mkuze, 24.i.1966 AcV66/76; 1 paratype from grass Park Rynie, 31.i.1966 AcV66/141, about 100 other specimens from the Natal coast, all T.J. Coates leg.	Holotype and 4 paratypes, NIC	
Sinella coeca (Schött, 1896)	Goto 1953	WC	I?	Cango Caves, nr Oudtshoorn (J.S. Harington & I.J. Lewis leg) - see Harington (1952) - in abundance in first mile and half of cave in rotting wood, moss, on rocks and stalagmites, and in very high numbers on floor of main chamber on bat guano.	Deposited in SAMC, also possession of collectors and author	Qu, Zhang & Chen (2010)
Sinella hofti Schäffer, 1896	Paclt 1959	WC	I	Groot Swartberg Mountain Range, Cango Caves, 19.x.1948 (3 specimens), B. Hanstrom leg, - ibidem in central part of cave, 6.1.1951 (1 specimen), SSAE leg. Loc 121.	Museum Lund	
Isotomidae						
Archisotoma sabulosa Barra, 1997	Barra 1997	KZN	E	Sand under pioneer plants 5 cm deep, 03.ii.1992, J.-P. Rieb leg.	Holotype ♀, one paratype and two	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					other specimens, MNHN	
Arlea tridens Barra, 1997	Barra 1997	KZN	E	Sodwana Bay National park, litter and superficial humus of dunes next to dense forest, 02.ii.1992, J.-P. Rieb leg.	Holotype ♀, one paratype and two other specimens, MNHN	
Ballistura schoetti Dalla Torre, 1895	Yosii 1959	WC	I	Beach of Rondevlei Marsh, 10.iii.1958, 25 specimens.		
Ballistura schoetti (Dalla Torre, 1895)	Paclt 1967	WC	I	Mamre Road, Waterkloof Farm, July 1937, D.v.V. Webb leg.	14 specimens NIC	*Proisotoma schötti* Dalla Torre, 1895
Ballistura schoetti (Dalla Torre, 1895)	Paclt 1967	EC		Graaff-Reinet 29.ix.1939, D.v.V. Webb leg.	23 specimens NIC	
Ballistura schoetti (Dalla Torre, 1895)	Paclt 1959	WC	I	Cape Flats, 1 M east of Zeekoeivlei, among dense vegetation at freshwater pool, 8.12.1950, SSAE leg., loc 76.	1 specimen Museum Lund	
Ballistura schoetti (Dalla Torre, 1895)	Womersley 1934	WC	I	Stellenbosch, 28.viii.1927 Dr Hesse leg.		
Cryptopygus caecus Wahlgren, 1906	Paclt 1959	KZN	E	Champagne Castle, Drakensberg, Feb 1946 (2 specimens), R. F. Lawrence leg.		
Cryptopygus caecus Wahlgren, 1906	Paclt 1959	WC	E	Cape Peninsula, Table Mountain, Wynberg Cave Ravine, sieved from wet vegetable debris, alt 2400 ft., 18.xii.1950, SSAE leg., loc. 84	2 specimens Museum Lund	
Cryptopygus riebi Barra, 1997	Barra 1997	KZN	E	Sodwana Bay, sand under pioneer plants 5 cm deep, 03.ii.1992, J.-P. Rieb leg.	Holotype ♀ paratype and two other preparations, MNHN	
Folsomides americanus Denis, 1931	Paclt 1959	KZN	I	Champagne Castle, Drakensberg, Feb 1946 (3 specimens), Pietermaritzburg, garden, from dry leaves, Sept 1951 (1 specimen), all R.F. Lawrence leg.		
Folsomides americanus Denis, 1931	Barra 1997	KZN	I	Sodwana Bay		
Folsomina onychiurina Denis, 1931	Barra 1997	KZN	I	Sodwana Bay		
Isotoma finitima (Ščerbakov,	Paclt 1959	KZN	I	Champagne Castle, Drakensberg, Feb 1946, R. F. Lawrence		*Folsomotoma*

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
1899)				leg (29 specimens).		*finitima* Ščerbakov, 1899
Hemisotoma thermophila (Axelson, 1900)	Paclt 1959	WC	I	Border 20 miles N of Matatiele (S. of Qacas Nek), 6500 ft. alt., at small rock pool, 08.iii.1951, loc 214 SSAE leg.	1 specimen Museum Lund	
Hemisotoma thermophila (Axelson, 1900)	Womersley 1934	KZN	I	Inchanga, Nov. 1917, K.H. Barnard leg.	1 young, poorly preserved specimen (noted by Paclt 1959)	
Hemisotoma thermophila (Axelson, 1900)	Coates 1970	WC	I	Tsitsikama Forest and Coastal National Park, under fallen oak leaves, near conservator's house and under rotting leaves, Storm River Mouth.		*Isotoma thermophila* Axelson, 1900
Isotomiella sodwana Barra, 1997	Barra 1997	KZN	E	Sodwana Bay National Park, litter and humus on surface of sand dunes, 02.ii.1992, J.-P. Rieb leg.	Two copies of holotype (sex not visible), MNHN	
Isotomodes productus (Axelson, 1906)	Womersley 1934	WC	I	Signal Hill, Cape Town, under stones, 31.viii.1930 (Womersley leg).		
Isotomurus palustris (Müller, 1776)	Paclt 1959	WC	I	Table Mountain, Stellenbosch (from Womersley 1934).	2 specimens in SAMC labelled *Isotoma mauretanica*	*Identification to check, Isotomurus genus needs revision, see Carapelli ref.*
Isotomurus palustris (Müller, 1776)	Paclt 1967	WC	I	Mamre Road, Waterkloof Farm, 3.vii 1937, 6 specimens AcV28; Gordon's Bay, Steenbras River Mouth, moss and rotten leaves, 1.viii.1937, 1 specimen AvV31, 4.viii.1937, 7 specimens AcV34 and 11.viii.1937, 17 specimens AcV40; Somerset West, Sit Lowrys Pass, 12.viii.1937, 1 specimen, AcV41; gordons Bay, 5.viii.1938, 20 specimens AcV55, all D.v.V. Webb leg.	NIC	
Isotomurus palustris (Müller, 1776)	Paclt 1967	EC	I	Uitenhage, Prickly Pear Laboratory, on banks of Swartkops River, 3.xi.1938, 1 specimen Ac61, Abderdeen, 21.xi,1939, 15 specimens AcV68, all D.v.V. Webb leg.	NIC	
Isotomurus palustris (Müller, 1776)	Paclt 1967	G	I	Pretoria, Parktown, grass on banks of Apies River, 24.ix.1937, 1 specimen, AcV45 D.v.V. Webb leg.		
Isotomurus palustris (Müller, 1776)	Paclt 1967	KZN	I	Mkuzi Game Reserve, Zululand, light traps, D. v. V. Webb leg, December 1945 to January 1946, 1 specimen AcV82.	NIC	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Isotomurus palustris (Müller, 1776)	Womersley 1934	WC	I	Ceres, Oct 1927 (K.H. Barnard leg).		
Isotomurus palustris var. *balteata* Reuter, 1876	Womersley 1934	WC	E?	Table Mountain Cape Town, 12.ix.1913 K.H. Barnard leg, Stellenbosch 29.viii.1927 Dr, Hesse leg.		
Isotomurus tricuspis Börner, 1906	Paclt 1959	WC	?	Cape Town, Table Mountain, also three juvenile specimens from Rondebosch, 29.vii.1930, H. Womersley leg.	from slide in SAM, 1 specimen	
Isotomurus tricuspis Börner, 1906	Paclt 1967	WC	?	Table Mountain Drive Waterfall no. 2, damp moss, 5.v.1956, 2 specimens AcV106, D.v.V. Webb leg.	NIC	
Micranurophorus musci Bernard, 1977	Barra 1997	KZN	I	Sodwana Bay, humid sand 20 cm deep under pioneer vegetation, 06.ii.1992, J.-R. Rieb leg.		
Parisotoma mossopi (Womersley, 1934)	Paclt 1959	FS	E	Bloemfontein, under few pine trees, from soil containing large amounts of organic material, April 1957 (1 specimen), R. van Pletzen leg.		Described from Southern Namibia as *Isotoma mossopi*.
Parisotoma notabilis (Schäffer, 1896)	Paclt 1959	WC	I	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 SSAE leg. Loc. 79 (2 specimens), Table Mountain, Wynberg Cave Ravine, sieved from wet vegetable matter, alt 2400 ft., 18.xii.1950, SSAE leg. Loc 84 (69 specimens)., Houtbay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, alt 600 ft., 18.i.1951, loc 161 (1 specimen).	Museum Lund	
Parisotoma notabilis (Schäffer, 1896)	Paclt 1967	WC	I	Van Rhynsdorp Knersvlakte, 3 miles form Van Rhyns Pass, 22.iii.1956, 17 specimens AcV93; Hout Bay, Chapmans Peak Drive, damp soil and moss, 22.iv.1956, 1 specimen AcV102, Table Mountain Drive, humus and pine needles, 5.v.1956, 13 specimen AcV105, Idem, Table Mountain Drive waterfall no. 2, damp moss, 5.v.1956, 10 specimens AcV106, all material D.v.V. Webb leg.	NIC	
Parisotoma obscurocellata Potapov, Janion and Deharveng, 2011	Potapov, Janion & Deharveng 2011	WC	E	Type locality: Western Cape, South Africa, Betty's Bay, 11.iii.2008, under creeping plants, extraction in Berlese funnels, legs. L. Deharveng and A. Bedos, SAF063.	Holotype ♀ on slide and about 60 paratypes (12 on slide, 48 in alcohol), holotype and 20 paratypes kept at SAMC and 20	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					paratypes in MNHN	
Parisotoma sexsetosa Potapov, Janion and Deharveng, 2011	Potapov, Janion & Deharveng 2011	WC	E	Type locality: Table Mountain National Park, 10.iii.2009, native forest, sieving and extraction from Berlese funnel, near Wynberg cave, SAF141m L. Deharveng & A. Bedos leg, RSA09_TBM001 C. Janion leg., near inchuk cave entrance SAF144 (LD & AB).	Holotype ♀ , about 1560 paratypes, Holotype ♀ and 140 paratypes SAMC, 140 paratypes in MNHN, 140 paratypes in MSPU	
Proisotoma africana (Womersley, 1934)	Paclt 1959	WC	E	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 SSAE leg. Loc. 79.	8 specimens Museum Lund	*Clavisotoma africana* Womersley, 1934
Proisotoma africana (Womersley, 1934)	Womersley 1934	WC	E	Rain pools in Kimberley, Feb 1915 Miss Witman leg, rain pools Cape Town June 1915 K.H. Barnard leg.	Co-types in the SAMC	
Proisotoma davidi Barra, 2001	Barra 2001	EC	E	Amatola Mountains, Themeda grassland soils at Hogsback, 1600 m a.s.l., David Marshall leg.	Holotype female and three paratypes, MNHN	
Proisotoma minuta (Tullberg, 1871)	Womersley 1934	WC	I	Table Mountain Cape Town 4 June 1913 (K.H. Barnard leg), Stellenbosch 7.vii.1930 (Womersley leg).	Two specimens observed by Paclt 1959 in SAMC, observed to be *Isotomurus palustris,* but lack trichobothria.	*Isotoma mauretanica* Handschin, 1926
Proisotoma minuta (Tullberg, 1871)	Paclt 1959	KZN	I	Pietermaritzburg, from dry leaves in garden, Sept 1951, R.F. Lawrence, 6 specimens.		
Proisotoma minuta (Tullberg, 1871)	Paclt 1959	WC	I	Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 10.xii.1950 Loc. 79, SSAE leg.	30 specimens Museum Lund	
Proisotoma minuta (Tullberg, 1871)	Paclt 1959	FS	I	Bloemfontein, under few pine trees, from soil containing large amounts of organic material, April 1957 (1 specimen), R. van Pletzen leg., Bloemfontein district, garden, from soil containing large amount of organic plant material, August 1957, R. van Pletzen leg. (4 specimens).		
Proisotoma minuta (Tullberg, 1871)	Paclt 1959	EC	I	Dordrecht district, from heap of decomposing mealie cobs, July and October 1957, R. van Pletzen leg, about 60		

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
				specimens.		
Proisotoma minuta (Tullberg, 1871)	Paclt 1967	EC	I	Queenstown, 22.iii.1939, A number of body wracks AcV67.	NIC	
Proisotoma minuta (Tullberg, 1871)	Paclt 1967	WC	I	Simonstown, Red Hill Drive, damp soil and moss, 15.iv.1956, 1 specimen AcV101, D,v.V. Webb leg, Idem, Municipal Centre, soil in colony of *Coptotermes formosanus* Shiraki in the Termite Research Laboratory of the Division of Entomology, Simonstown, 9.viii.1956, 1 specimen, AcV107, Mrs P.E. de Wet leg.	NIC	
Paronellidae						
Dicranocentruga nigromaculata Schött, 1903	Paclt 1959	KZN	E	Champagne Castle, Drakensberg, Feb 1946, R.F. Lawrence leg, 25 specimens.		Dubious, also recorded for Brazil?
Tomoceridae						
Neophorella dubia Womersley, 1934*	Womersley 1934	WC	E	Table Mountain, Cape Town, 2500 feet, 12.ix.1913, K.H. Barnard leg	1 specimen SAMC, slide in bad condition.	Not found again.
NEELIPLEONA						
Neelidae						
Megalothorax minimus (Willem, 1900)	Paclt 1967	WC	I	Hout Bay, Chapman's Peak Drive, damp soil and moss, 15.iv.1956, 16 specimens, AcV99; Table Mountain Drive Waterfall No. 2, damp moss, 5.v. 1956, 6 specimens, AcV106, all D.v.V. Webb leg.	National Collection of Insects, Pretoria	
SYMPHYPLEONA						
Bourletiellidae						
Bourletiella schultzei Börner, 1908	Börner 1908	NC	E?	Steinkopf and Kamaggas, Spring 1904, L. Schultze leg.		
Deuterosminthurus marmoratus (Womersley, 1931)	Womersley 1931	WC	E	Hottentots Holland Mountains, Jan 1916, K.H. Barnard leg., rain pools at 4000 ft.; and top of Kalk Bay Mountain, Cape Peninsula, 12.i.1912.	Co-types in SAMC	*Prorastriopes marmoratus* Womersley, 1931
Prorastriopes webbi Paclt 1964	Paclt 1964	KZN	E	Mkuzi Game Reserve, Zululand, found at light, D. v. V. Webb leg, December 1945 to January 1946.	Holotype ♀, SMF A 1673, Paratypes 2 ♀, NIC AcV 82,	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					Natural History Museum, Entomology Section, Frankfurt	
Prorastriopes webbi Paclt 1964	Coates 1970	MP	E	Kruger National Park, under rotting leaves of *Bougainvillea* sp. Shingwidzi Rest Camp		
Prorastriopes webbi Paclt 1964	Coates 1970	EC	E	Mountain Zebra National park, on *Diospyros austrafricana* var. *microphylla* and on unidentified shrub on top of mountain near beacon.		
Rastriopes lineata Womersley, 1931	Womersley 1931	WC	E	Under fallen twig. Kloof Nek, Cape Town, 27.vii.1930. Also 4 immature specimens from surface of rain pools in Cape Town, K.H. Bernard leg, 09.v.1916.	Holotype in SAMC	Paclt (1959) syn. *Rastriopes schultzei*
Rastriopes lineata Womersley, 1931	Paclt 1967	WC	E	Mamre Road, Waterkloof Farm, 3.vi.1937, 1 specimen AcV28; Gordons Bay, Steenbras River Mouth, moss and rotten leaves 1.viii.1937, 1 specimens AcV31, Gordons Bay, 4.viii.1937, 2 specimens AcV34, 1 specimen AcV 40 and 13.viii.1937, 2 specimensAcV42, Palmiet River near Kleinmond, 17,viii,1937, 1 specimen, AcV44, all D.v.V. Webb leg.	NIC	
Rastriopes lineata Womersley, 1931	Paclt 1967	G	E	Pretoria, Parktown, grass on banks of Apies River, 24.ix.1937, 2 specimens, AcV45, D.v.V. Webb leg	NIC	
Rastriopes lineata Womersley, 1931	Paclt 1967	NC	E	Graaff-Reinet 29.ix.1939, 6 specimens AcV73, D.v.V. Webb leg.	NIC	
Rastriopes schultzei Börner, 1908	Paclt 1959	WC	PT	Hangklip, 14 miles S of Strand, under stone on dry *Juncus* heath, 19.xii.1950, SSAE leg, loc. 86, Maanschijnkop (Maanskynkop?), 7 miles E of Hermanus, swept in dry vegetation, heath, 21.12.1950, SSAE leg. Loc. 93, Table Mountain, swept among vegetation, Juncus tufts, alt 3400 ft., 7.xii.1951, SSAE leg, loc.353.	16 ♀ specimens, Museum Lund	
Tritosminthurus schuhi Snider, 1988*	Snider 1988	WC	E	Cape Province, Cape Point Nature Reserve, 30.i.1968, R.T. Schuh, J. and S. Slater and M. Sweet legs.	Holotype ♀, 100+ co-types, 31 slides, all deposited in Entomology Museum, Michigan	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					State University	
Dicyrtomidae						
Dicyrtomina minuta africana Womersley, 1931	Womersley 1931	WC	E?	Elsenburg, on native olive bushes, 24.vii.1930, 28.viii.1927 leg Dr. Hesse.		
Dicyrtomina minuta O. Fabricius, 1783	Paclt 1959	WC	I	Kirstenbosch, at stony stream, shaded by dense vegetation, 6.vii.1951, SSAE leg. Loc. 352.	4 specimens Museum Lund	
Dicyrtomina minuta O. Fabricius, 1783	Paclt 1967	WC	I	Somerset West, 4.viii.1937, 26 specimens AcV33; Gordon's Bay, 10.viii.1937, 20 specimens AcV38; Palmiet River near Kleinmond 17.viii.1937, 5 specimens AcV44; Gordon's Bay 5.viii.1938, 1 specimen AcV55, all D.v.V. Webb leg.	NIC	
Katiannidae						
Katianna kerguelensis Denis, 1947	Paclt 1959	KZN	?	Champagne Castle, Drakensberg, R. F. Lawrence leg, Feb 1946, 1 specimen.	Paclt found 1 specimen in vial in SAMC from Womersley collection, maybe from SW Cape or S. Zimbabwe.	Dubious, has a sub-Antarctic distribution (Greenslade 2004, Bellinger et al. 2012)
Sminthurinus niger (Lubbock, 1873)	Womersley 1931	WC	I	Stellenbosch, under loose bark of fallen log, C.P., 12.viii.1930.		
Sminthurinus pallidus Womersley, 1931	Womersley 1931	WC	E	Type locality: Stellenbosch, surface of ground beneath strong grow of *Cryptostemma calendulaceum* (Cape weed) in Stellenbosch University orchard, 28.xiii.1930	Holotype in SAMC	
Sminthurinus stenognathus (Börner, 1907)	Paclt 1959	WC	Africa & Brazil	Franschhoek Forest Reserve, Upper Berg river, at stream, alt 1500 ft., 1.xi.1950, SSAE leg, loc 21 (1 specimen), Cape Peninsula, Cape Point Nature Reserve, sieved from wet leaves in low bush, 2400 ft., 18.xii.1950 Loc. 84 (9 specimens), Hout Bay, Skoorsteenkop, sieved from vegetable debris in dense indigenous forest, 600 ft., 28.i.1951, loc. 161 (14 specimens), all SSAE leg.	Museum Lund	*Stegnognathellus stenognathus* (Börner, 1907) Mari Mutt JA & Bellinger, PF, 1990:144
Sminthurinus stenognathus (Börner, 1907)	Paclt 1959	KZN	E	Pietermaritzburg, dry leaves in garden, R.F. Lawrence Sept 1951, 61 specimens.		
Sminthurinus terrestris	Paclt 1967	WC	E	Paarl, fallen leaves, 29.viii.1937, 1 specimen, AcV29;	NIC	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
Womersley, 1931				Gordon’s Bay 9.viii.1937, 27 specimens AcV37, 11.vii.1937, 1 specimen AcV43; Strand, 11.viii.1937, 3 specimens AcV39, all D.v.V. Webb leg.		
Sminthurinus terrestris Womersley, 1931	Womersley 1931	WC	E	Stellenbosch, surface of ground beneath strong grow of *Cryptostemma calendulaceum* (Cape weed) in Stellenbosch University orchard, 24.vii.1930 and 22-24.viii.30; similar habitat Marsh Memorial Homes, Rondebosch, August, 1930.	Type in SAMC	
Papirinus prodigiosus Yosii, 1954	Paclt 1959	KZN	PT	Champagne Castle, Drakensberg, Feb 1946, R.F. Lawrence leg. (1 specimens).		
Sminthurididae						
Sminthurides serroseta Börner, 1908	Börner 1908	NC	PT	Kalahari, between the pans Sekgoma and Khakhea, November 1904, L. Schultze leg, ♂ very numerous, ♂ and ♀, found in thick clusters, L. Schultze leg.		
Sphaeridia minimus (Schött, 1893)	Paclt 1959	FS	I	Bloemfontein, garden, from soil containing large amount of organic plant material, August 1957, R. van Pletzen, 8 specimens.		
Sphaeridia minimus (Schött, 1893)	Paclt 1967	WC	I	van Rhynsdorp, Knersvlakte, 3 miles from van Rhyns pass, 22.iii.1956, , 1 ♂and 6 ♀, AcV93; Simons Town, Red hill Drive, damp soil and moss, 22.iv.1956, 2 ♀ AcV 101; Table Mountain Drive, humus and pine needles, 5.v.1956, 1 female AcV105, all D.v.V. Webb leg.	NIC	
Sminthuridae						
Sminthurus viridis (Linnaeus, 1758)	Lawrence 1953	?	I	No information given.		
Sminthurus viridis (Linnaeus, 1758)	Paclt 1959	WC	I	Somerset West, on oats, July 1941, Mally leg., Caledon, on Lucerne pastures, August 1956, Dept. Agric Stellenbosch leg.	Somerset West: 2 ♀ and 11 ♀ specimens in Dept. Agric. Stellenbosch, 11 ♀ specimens in author's collection, Caledon: 2 ♀ and 2 ♀ specimens at Dept. Agric.	

Current species name	Source	SA	Status	Records	Collection	Comments / Reference
					Stellenbosch, 16 ♀ and 20 ♀ specimens in author's collection.	
Papirinus prodigiosus Yosii, 1954	Paclt 1959	KZN	PT	Champagne Castle, Drakensberg, Feb 1946, R.F. Lawrence leg. (1 specimens).		

Table 2: Species list for the Western Cape from sampling (S) and accepted records from the literature (L). Barcoded species (B) which are known to be species are included here. See text for details.

Current	**Source**	**Location**
ENTOMOBRYOMORPHA		
Cyphoderidae		
Cyphoderus sp.	S	Widely distributed
Cyphoderus squamidives	L	Simon's Town
Entomobryidae		
Capbrya sp.	S	Table Mountain
Drepanura sp.	S	Rooiels
Entomobrya atrocincta	L	Paarl
Entomobrya multifasciata	S	Widely distributed
Entomobrya nivalis	S	Cape Town
Entomobrya sp. 1	S	Cederberg Wilderness Area
Entomobrya sp. 2	S	Cederberg Wilderness Area
Entomobrya sp. 3	S	Grootbos
Entomobrya sp. 4	S	Kalk Bay, Grootbos
Entomobrya sp. 5	S	Paternoster
Lepidocyrtoides sp.	S	Helderberg
Lepidocyrtus lanuginosus	L	Table Mountain
Lepidocyrtus sp. 1	S	Wilderness NP
Lepidocyrtus sp. 2	S	Helderberg
Lepidosira sp.	S	Jonkershoek NR
Pseudosinella octopunctata	L	Table Mountain
Pseudosinella sp. 1	S	Jonkershoek
Pseudosinella sp. 2	S	Table Mountain
Pseudosinella sp. 3	S	Wilderness NP
Seira annulicornis	L	Table Mountain
Seira annulipes	L	Keeromberg
Seira barnardi	L & S	Orange Kloof, widespread
Seira capensis	L	Widespread
Seira dayi	L	Skeleton Gorge, Grootvadersbosch
Seira flavovirens	L	Franschhoek
Seira grisea	L	Kirstenbosch, Swellendam
Seira lindei	L	Heidelberg
Seira marephila	L	Widespread
Seira mathewsi	L	Swellendam
Seira metala	L	Grootvadersbosch
Seira nagatai	L	Table Mountain
Seira pseudocoerulea	L	Table Mountain
Seira rowani	L	Table Mountain, Tsitsikama
Seira rykei	L	Grootvadersbosch
Seira sp. 01	S & B	Wilderness NP
Seira sp. 02	S	Wilderness NP
Seira sp. 03	S	Wilderness NP

Current	**Source**	**Location**
Seira sp. 04	S & B	Cederberg Wilderness Area
Seira sp. 05	S	Grootbos
Seira sp. 06	S & B	Jonkershoek
Seira sp. 07	S	Grootbos, Jonkershoek
Seira sp. 08	S & B	Jonkershoek, Table Mountain
Seira sp. 09	S	Wilderness NP
Seira sp. 10	S & B	Jonkershoek
Seira sp. 11	S	Grootbos
Seira sp. 12	S	Helderberg, Jonkershoek, Table Mountain
Seira sp. 13	S	Paternoster
Seira sp. 14	S	Grootbos
Seira sp. 15	S	Grootbos
Seira sp. 16	S & B	Wilderness NP
Seira sp. 17	S	Jonkershoek, Table Mountain
Seira sp. 18	S	Grootbos
Seira sp. 19	S	Grootbos
Seira sp. 20	S	Grootbos
Seira sp. 21	S	Helderberg
Seira sp. 22	B	Oudtshoorn
Seira sp. 23	B	Stellenbosch
Seira sp. 24	B	Bredasdorp
Seira tsikama	L	Tsitsikama
Sinella coeca	L	Oudtshoorn
Sinella hofti	L	Oudtshoorn
Sinella sp.	S	Simondium
Willowsia sp.	B	Helderberg
Willowsia nigromaculata	S	Stellenbosch
Isotomidae		
Archisotoma sp. 1	S	Betty's Bay
Archisotoma sp. 2	S	De Kelders, Cape Point
Ballistrura schoetti	L & S	Cape Town
Cryptopygus caecus	L & S	Widespread
Cryptopygus sp. 1	S	Betty's Bay
Cryptopygus sp. 2	S	Helderberg
Cryptopygus sp. 3	S	
Cryptopygus sp. 4	S	Jonkershoek
Cryptopygus sp. 5	S	
Cryptopygus sp. 6	S	Table Mountain
Desoria sp.	S & B	Widely distributed
Folsomia candida	S	Wilderness NP, Simondium
Folsomides americanus	S	Widely distributed
Folsomides parvulus	S	Widely distributed
Folsomina onychiurina	S	Rooiels
Halisotoma sp.	S	Rooiels
Hemisotoma sp. 1	S	Betty's Bay

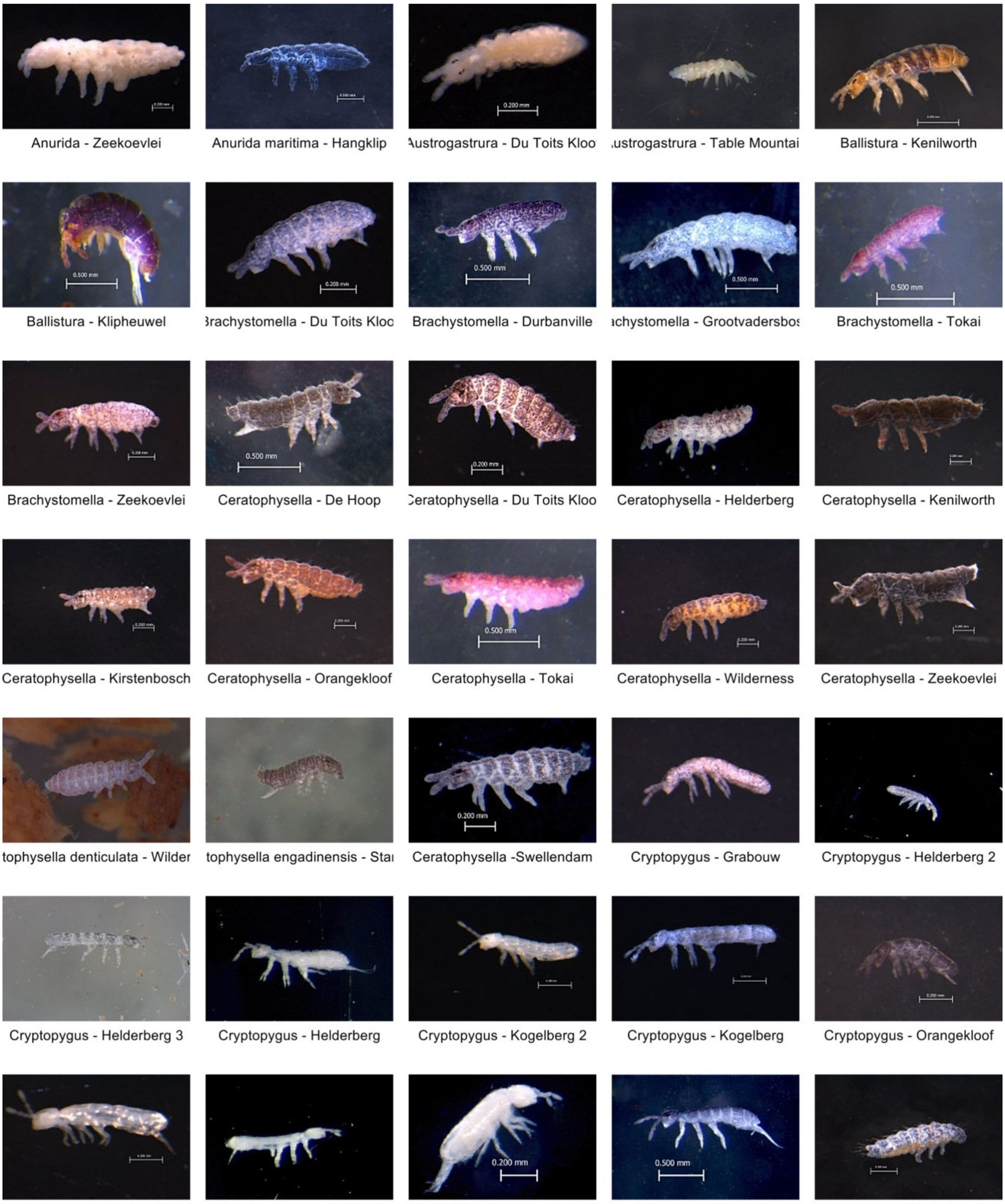
Current	**Source**	**Location**
Hemisotoma sp. 2	S	Rooiels
Hemisotoma thermophila	L	Tsitsikama
Isotoma sp. 1	S	Helderberg
Isotoma sp. 2	S & B	Helderberg
Isotoma sp. 3	S	Jonkershoek
Isotoma sp. 4	S	Orange Kloof, Table Mountain
Isotoma sp. 5	S	Stanford
Isotomiella minor	S	Helderberg
Isotomodes productus	L	Cape Town
Isotomurus maculatus	S & B	Tokai
Isotomurus palustris	L & S & B	Widespread
Isotomurus plumosus	S	Wilderness NP
Isotomurus unifasciatus	S & B	Stanford
Micranurophorus sp.	S	Grootbos
Parisotoma obscurocellata	L	Betty's Bay
Parisotoma sexsetosa	L & B	Table Mountain
Parisotoma sp. 1	S	Jonkershoek
Parisotoma sp. 2	S	
Parisotoma sp. 3	S	Jonkershoek pine
Parisotoma sp. 4	S	
Parisotoma sp. 5	S	
Parisotoma sp. 6	S	
Proisotoma africana	L	Cape Point
Proisotoma minuta	L & S	Widely distributed
Proisotomodes bipunctatus	S	Stanford
Proisotomodes sp.	S	Kalk Bay
Microfalculidae		
Microfalcula sp.	S	Grootbos
Oncopoduridae		
Oncopodura sp.	S	Table Mountain
Paronellidae		
Paronellidae sp.	S	Helderberg
Tomoceridae		
Neophorella dubia	L	Table Mountain
Tomocerus sp.	S	Helderberg
NEELIPLEONA		
Neelidae		
Megalothorax minimus	L	Cape Town
Megalothorax sp. 1	S	De Kelders
Neelus sp.	S & B	Widely distributed
PODUROMORPHA		
Brachystomellidae		
Brachystomella coatesi	L	Saasveld
Brachystomella georgensis	L &S	Jonkershoek, Saasveld
Brachystomella parvula (	L	Widespread

Current	Source	Location
Brachystomella parvula africana Yosii, 1959	L	Table Mountain
Brachystomella sp. 1	S	Table Mountain
Brachystomella sp. 2	S	Wilderness NP
Probrachystomellides nicolaii	L	Saasveld
Setanodosa capitata	L	Stellenbosch
Setanodosa sp. 1	S & B	Stellenbosch
Setanodosa sp. 2	S	Jonkershoek NR
Hypogastruridae		
Austrogastrura sp.	S & B	Table Mountain, Du Toit’s Kloof
Austrogastrura lobata	L	Table Mountain
Ceratophysella denticulata	S	Widely distributed
Ceratophysella engadinensis	S	Helderberg
Choreutinula sp.	S	Jonkershoek
Hypogastrura manubrialis	L & S	Piketberg
Hypogastrura purpurescens	L	Cape Town
Hypogastrura	L	Franschhoek
Mesogastrura libyca	L	Cape Point
Schoettella sp.	S	Kogelberg
Triacanthella madiba	L,B, S	Table Mountain
Triacanthella sp. 1	S & B	Du Toitskloof, Kogelberg
Triacanthella sp. 2	S	Orange Kloof
Willemia buddenbrocki	S	Betty's Bay, Table Mountain
Xenylla capensis	L	Saasveld
Xenylla maritima	L & S	Stellenbosch
Isotogastruridae		
Isotogastrura sp.	S	Wilderness beach
Neanuridae		
Aethiopella sp.	B	Stanford
Aethiopella flavoantennata capensis	L & S	Widely distributed
Anurida cf. *granaria*	S & B	Cape Town
Anurida maritima	L,B, S	Pringle Bay
Deutonura gibbosa	S	Simondium, Silvermine
Ectonura barrai	L & S	Grootvadersbosch
Ectonura monochaeta	L & S	Jonkershoek, Table Mountain area
Ectonura natalensis	L	Houtbay
Ectonura sp. 1	S	Jonkershoek
Ectonura sp. 2	S	Helderberg
Ectonura sp. 3	S	Jonkeshoek
Ectonura sp. 4	S	Piketberg
Friesea claviseta	S & L	Betty's Bay, Stellenbosch
Friesea sp. 1	S	Cape of Good Hope
Friesea sp. 2	S	Wilderness NP
Linnaniemia sp.	S	Jonkershoek NR
Micranurida pygmaea	S	Helderberg

Current	**Source**	**Location**
Oudemansia sp.	S	De Kelders
Paleonura sp.	S	Jonkershoek NR
Pseudachorutella africana	L	Saasveld
Pseudachorutes parvulus	S	Helderberg
Pseudachorutes sp. 1	S	Helderberg
Pseudachorutes univesicatus	L	Saasveld
Pseudachorutinae sp. 1	S	Stanford
Pseudachorutinae sp. 2	S	Kalk Bay
Stachorutes sp.	S	Grootbos
Vitronura sp.	S & B	Malmesbury (L1), Wildernesss
Odontellidae		
Afrodontella sp. 1	S	Kalk Bay
Afrodontella sp. 2	S	Grootbos
Odontella sylvatica	L	Saasveld
Stachia sp.	S	Table Mountain area
Superodontella sp.	S	Helderberg
Onychiuridae		
Deuteraphorura sp.	S	Helderberg
Orthonychiurus saasveldensis	L	Saasveld
Orthonychiurus sp.	S	Widely distributed
Thalassaphorura sp.	B & S	Stanford (L2)
Tullbergiidae		
Delamarephorura capensis	S	Betty's Bay
Fissuraphorura miscellana	S	Jonkershoek NR
Mesaphorura critica	S	Betty's Bay, Rooiels
Mesaphorura krausbaueri	S & L	Jonkershoek
Mesaphorura macrochaeta	S	Betty's Bay, Jonkershoek, Table Mountain
Mesaphorura yosii	S	Du Toitskloof
Multivesicula sp.	S	Cape of Good Hope
Paratullbergia callipygos	L	Cape Town
Prabhergia	S	Orange Kloof
Tillieria sp.	S	Jonkershoek NR
Tullbergia bisetosa	S	Jonkershoek NR
Tullbergia kilimandjarica	S & L	Betty's Bay
Tullbergia meridionalis	S	Jonkershoek NR
SYMPHYPLEONA		
Arrhopalitidae		
Arrhopalites sp.	S	Grootvadersbosch, Jonkershoek
Bourletiellidae		
Bourletiellidae sp. 1	S	Grootbos
Bourletiellidae sp. 2	S	Grootbos
Deuterosminthurus marmoratus	L	Kalk Bay, Hottentots Holland
Rastriopes lineata	L	Widespread
Rastriopes schultzei	L	Hermanus, Hangklip, Table Mountain
Tritosminthurus schuhi	L	Cape Point

Current	**Source**	**Location**
Dicyrtomidae		
Dicyrtomina sp.	S	Stellenbosch
Dicyrtomina minuta africana	L	Elsenburg
Dicyrtomina minuta	L	Widespread
Katiannidae		
Sminthurinus bimaculatus	S	Jonkershoek NR, Kogelberg, Helderberg
Sminthurinus elegans	S	Tokai, Jonkershoek
Sminthurinus niger	L & S	Stellenbosch & Wilderness NP
Sminthurinus pallidus	L	Stellenbosch
Sminthurinus stenognathus	L	Widespread
Sminthurinus terrestris	L	Stellenbosch, Rondebosch
Mackenziellidae		
Mackenziella sp.	S	Tokai
Sminthuridae		
Pararrhopalites sp.	S	Table Mountain
Sminthurus viridis	L	Somerset West, Caledon
Sminthurididae		
Sphaeridia minimus	L	Widespread
Sphaeridia sp.	S	Widely distributed

Fig. 1: Examples of springtail specimens successfully barcoded, displayed in alphabetical order with the locality from where it was collected.



Anurida - Zeekoevlei
Anurida maritima - Hangklip
Austrogastrura - Du Toits Kloo
ustrogastrura - Table Mountai
Ballistura - Kenilworth
Ballistura - Klipheuwel
Brachystomella - Du Toits Kloo
Brachystomella - Durbanville
achystomella - Grootvadersbos
Brachystomella - Tokai
Brachystomella - Zeekoevlei
Ceratophysella - De Hoop
Ceratophysella - Du Toits Kloo
Ceratophysella - Helderberg
Ceratophysella - Kenilworth
Ceratophysella - Kirstenbosch
Ceratophysella - Orangekloof
Ceratophysella - Tokai
Ceratophysella - Wilderness
Ceratophysella - Zeekoevlei
tophysella denticulata - Wilder
tophysella engadinensis - Sta
Ceratophysella -Swellendam
Cryptopygus - Grabouw
Cryptopygus - Helderberg 2
Cryptopygus - Helderberg 3
Cryptopygus - Helderberg
Cryptopygus - Kogelberg 2
Cryptopygus - Kogelberg
Cryptopygus - Orangekloof
Cryptopygus - Zeekoevlei
ryptopygus caecus - Helderbe
phoderidae - Grootvadersbos
Desoria - Wilderness
Deutonura - Kirstenbosch


Dicyrtomina - Kirstenbosch


Dicyrtomina - Stellenbosch

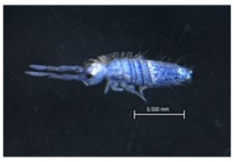

Dicyrtomina - Tokai


Ectonura - Stellenbosch


Ectonura - Table Mountain 2


Ectonura - Table Mountain

Entomobrya - De Hoop


Entomobrya - Jonkershoek


Entomobrya - Kogelberg

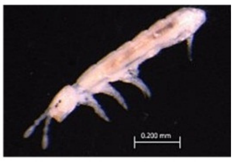
Entomobrya - Stanford

Entomobrya - Tokai


Entomobrya - Zeekoevlei


Folsomia - Stellenbosch

olsomides - Grootvadersbosc



Folsomides - Stanford


olsomides parvulus - Stanfor

Folsomides_GVB


Friesea - Malmesbury


Friesea - Rooiels

Hemisotoma - KwaZulu-Natal

Hemisotoma - Durbanville


Hemisotoma - Rooiels


Hemisotoma - Stanford


Hemisotoma - Zeekoevlei

Hypogastrura - Durbanville


Hypogastura - Zeekoevlei


Isotoma - Helderberg


Isotoma - Orangekloof 2

Isotoma - Orangekloof

Isotomodes - Hogsback


Isotomodes - Malmesbury

Isotomurus - Durbanville


Isotomurus - Grabouw


Isotomurus - Helderberg

Isotomurus - Stellenbosch

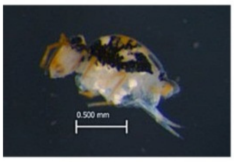
Isotomurus - Tokai

Isotomurus maculatus - Tokai

tomurus unifasciatus - Stanfor

tomurus unifasciatus - Stanfor

otomurus unifasciatus - Stanfo



atiannidae - Grootvadersbosc

Katiannidae - Stellenbosch

Katiannidae - Wilderness

Lepidocyrtinae - Stellenbosch

Lepidocyrtinae - Wilderness

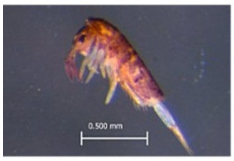
Lepidocyrtus - Bottelary

Lepidocyrtus - Helderberg

Lepidocyrtus - Kirstenbosch

Lepidocyrtus - Kogelberg

Lepidocyrtus - Malmesbury

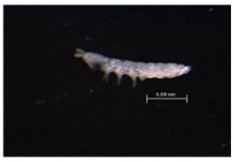


Lepidocyrtus - Tokai

Lepidocyrtus - Wilderness

Megalothorax - Kirstenbosch

Megalothorax - Orangekloof



Mesaphorura - Kirstenbosch

esaphorura - Table Mountai

Mesaphorura - Zeekoevlei

Micranurida - Stellenbosch

Neelus - Grabouw

Neelus - Kirstenbosch

Neelus 2 - Kirstenbosch

Onychiuridae - Wilderness

Orthonychiurus - Kirstenbosch

Orthonychiurus - Stanford

Paleonura - Wilderness

Parisotoma - Bottelary

Parisotoma - De Hoop

Parisotoma - Grabouw

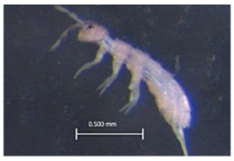
arisotoma - Grootvadersbosc

Parisotoma - Stanford

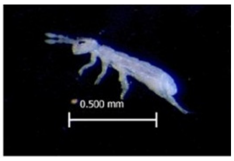

Parisotoma - Stellenbosch


Parisotoma - Table Mountain 2


Parisotoma - Table Mountain



Parisotoma - Tokai



Parisotoma - Wilderness 2


Parisotoma -Du Toits Kloof


Paronellidae - Helderberg


Paronellidae - Wilderness


Pseudachorutes - Rooiels 2


Pseudachorutes - Rooiels

Pseudachorutinae - Standford


seudachorutinae - Stellenbosc

Pseudosinella - De Hoop


Pseudosinella - Orangekloof

Seira - Bredasdorp

Seira - Cederberg

Seira - De Hoop 1

Seira - De Hoop 2

Seira - De Hoop 3

Seira - De Hoop 4


Seira - Grabouw 2

Seira - Grootvadersbosch 1

Seira - Grootvadersbosch 2


Seira - Helderberg 1


Seira - Helderberg 2


Seira - Kirstenbosch


Seira - Kogelberg 2


Seira - Kogelberg

Seira - Orangekloof

Seira - Oudtshoorn


Seira - Stellenbosch 2


Seira - Stellenbosch


Seira - Stellenbosch


Seira - Table Mountain

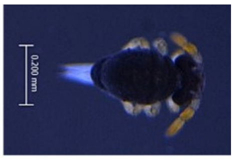

Seira - Wilderness 1

Seira - Wilderness 2

Setanodosa - Stellenbosch

Sminthurinus - Kenilworth

Sminthurinus - Orangekloof

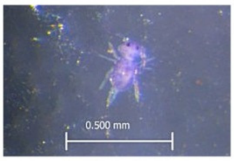


Sminthurinus - Stellenbosch

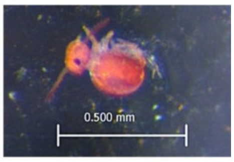
Sminthurinus - Tokai

Sminthurinus elegans - Tokai

Sphaeridia - Malmesbury



Sphaeridia - Tokai 2



Sphaeridia - Tokai

Triacanthella - Du Toits Kloof

Triacanthella - Jonkershoek

Triacanthella - Kogelberg

riacanthella - Table Mountain

Tullbergia - Helderberg

Tullbergia - Table Mountain

Vitronura - Malmesbury

Willowsia - Helderberg

Xenylla - Bottelary

Xenylla - Kogelberg

Xenylla - Malmesbury

Xenylla - Orangekloof

Xenylla - Stellenbosch

Xenylla - Wilderness

Chapter 3

The genus *Ectonura*, Cassagnau 1980 in South Africa (Collembola: Neanuridae: Neanurinae), with a key to South African Neanurinae

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Introduction

Neanurinae Collembola are represented in tropical Africa by a large number of species in the tribe Paleonurini, and a single representative of the tribe Neanurini, the parthenogenetic species *Neanura muscorum* (Templeton 1835). However, only a few areas have been sampled outside the mountain ranges of Eastern Africa (Cassagnau 1991, 1996, 2000; Weiner and Najt 1998). In South Africa, only three genera and five species of Neanurinae have been recorded so far (Fig. 1): *Neanura* MacGillivray, 1893 with *N. muscorum*; *Vitronura* Yosii, 1969 with *V. joanna* (Coates, 1968), and *Ectonura* Cassagnau, 1980 with *E. natalensis* (Womersley 1934), *E. oribiensis* (Coates, 1968) and *E. coatesi* Barra, 1994. *Neanura muscorum* has been probably introduced from Europe, where all other species of the genus *Neanura* occur. The genus *Vitronura*, diversified in China, Sunda and western Pacific islands, has a single widespread species, *V. giselae* (Gisin 1950), that occurs both in the tropics and in gardens in Europe. Therefore, the presence of another distinct species isolated in South Africa requires confirmation, as *V. joanna* is morphologically very close to *V. giselae*. The genus *Ectonura*, limited to South Africa in the African continent, includes the only Neanurinae unambiguously native of South Africa; the genus is otherwise present in New Caledonia with 11 species (Deharveng and Bedos 2002), and an undescribed species is recorded from South Australia by Greenslade and Deharveng (1991).

Among the large amount of samples recently collected in the Western Cape Province in the frame of the Franco-South African PROTEA project "Uncovering Springtail Diversity in the South African Cape Floristic Region: a combined taxonomic and barcoding approach", we retrieved representatives of the three cited genera, including new *Ectonura* species, as well as a single species of a fourth genus, *Paleonura* Cassagnau, 1982. This confirms that the South Africa Neanurinae fauna is particularly poor compared to that of the East African mountains or Madagascar (Cassagnau 1996, 2000), or other Gondwana territories such as Australia (Greenslade and Deharveng 1991). Its richness in Neanurinae is actually similar to that of temperate areas of South America, where *N. muscorum* also occurs, together with a few endemic *Paleonura* (Cassagnau and Oliveira 1990).

Ectonura is therefore the most diversified genus of Neanurinae in southern Africa. Several undescribed species were present in our samples, mostly as isolated specimens. Two of them were collected in sufficient numbers to be described and this is done here: *Ectonura* *monochaeta* **sp. n.** from Table Mountain and *Ectonura barrai* **sp. n.** from Grootvadersbosch, both located in the Western Cape Province. This thesis chapter does not constitute the formal descriptions, which are published as the paper listed in the title footnote.

Abbreviations used

Type deposit – **IM**, Iziko Museum (Cape Town, South Africa); **MNHN**, Museum National d'Histoire Naturelle (Paris, France).

Chaetal arrangement and notation follow Deharveng (1983) and Smolis (2008).

Abbreviations used in species descriptions and tables:

Tubercles and chaetal groups – **Af**, antenno-frontal; **CL**, clypeal; **De**, dorso-external; **Di**, dorso-internal; **DL**, dorso-lateral; **L**, lateral; **Oc**, ocular; **So**, subocular; **VL**, ventro-lateral; **Ve**, ventro-external; **Vi**, ventro-internal; **Ag**, antegenital; **An**, anal.

Appendages – **Cx**, coxa; **Fe**, femur; **Fu**, furcal rest; **Scx2**, subcoxa 2; **Tita**, tibiotarsus; **Tr**, trochanter; **VT**, ventral tube.

Types of chaetae – **M**, macrochaeta; **me**, mesochaeta; **mi**, microchaeta; **S**, S-chaeta ("sensillum" *auct.*) ; **ms**, s-microchaeta.

Others – **omma**, ommatidia; **Abd.**, abdominal segment; **Ant.**, antennal segment; **Th.**, thoracic segment.

Key to South African species of Neanurinae

1. Three eyes on each side of the head, body blue-grey in colour ……………………………………………………………………………………………………***Neanura muscorum* (Templeton, 1835)** (temperate cosmopolitan species)

- Two eyes on each side of the head, body not blue……………………………………………………………**2**

2. Central area of head with 3 tubercles…***Vitronura joanna* (Coates, 1968)** (uncertain status)

- Central area of head with 2 tubercles …………………………………………………………………***Ectonura* 3**

3. Th. II to Abd. IV, dorso-internal tubercle of tergites with at least two chaetae…………**4**

- Th. II to Abd. IV, dorso-internal tubercle of tergites with one chaeta ……………………………………………………………………………………………………***E. monochaeta* sp. n.**

4. Chaeta A absent on head……………………………………………………………………………………………**5**

- Chaeta A present on head……………………………………………………………………………………………**6**

5*. Modified chaetae Ag on Abd. V of the male much shorter than lateral Ag, very thick, truncated, apically ciliated…………………………………………***E. oribiensis*** (Coates, 1968) (endemic)

- Modified chaetae Ag on Abd. V of the male as long as lateral Ag, thin, pointed, with several unequal distal cilia…………………………………………………………..*E. coatesi* **(Barra, 1994)** (endemic)

6. Five chaetae on each central group of chaetae on head (1/2Af+Oc), chaeta D absent; one chaeta Di on Abd. V (Di2 absent); tubercles Di of Abd. V fused on axis………………………………………………………………….***E. natalensis*** **(Womersley, 1934)** (endemic)

- Six chaetae on each central group of chaetae on head (1/2Af+Oc), chaeta D present; two chaetae Di on Abd. V (Di2 present); tubercles Di of Abd. V separate……………..***E. barrai*** **sp. n.**

* The only differential character unambiguously separating *E. coatesi* from *E. oribiensis* is the morphology of modified chaetae Ag in the male.

Taxonomy

Ectonura Cassagnau, 1980

Type species: *Achorutes natalensis* Womersley, 1934 (Natal, South Africa)

Ectonura monochaeta sp. n.

Figs 2-3, Table 1.

Type material. Holotype female on slide. South Africa: Western Cape, Cape Town, Table Mountain National Park, S33°58.661', E18°24.050', 10/03/2009, native broadleaved forest, sieving of litter and extraction on Berlese funnel, Louis Deharveng and Anne Bedos leg (SAF-141).

8 paratypes on slides (3 males, 4 females, 1 juvenile) and more than 50 in alcohol, same data as holotype — 1 male on slide, ibid, Table Mountain, collapse of New Year cave system, 07/03/2009, native forest, litter, Berlese extraction, Louis Deharveng and Anne Bedos leg (SAF-129) — 1 male and 1 female on slides, ibid, Table Mountain, in a collapse, 10/03/2009, native forest, soil, Berlese extraction, Louis Deharveng and Anne Bedos leg (SAF-139) — 1 male and 1 female on slides, 5 specimens in alcohol, ibid, Table Mountain, Inchuk cave entrance, 10/03/2009, native forest, litter, Berlese extraction, Louis Deharveng and Anne Bedos leg (SAF-144). Slides were studied under a Leica DM2000 compound microcope with phase contrast and drawings were made using a Leica drawing tube.

Type deposition. Holotype, 6 paratypes on slides (3 males, 3 females) and 25 paratypes in alcohol in IM; 7 paratypes on slides (3 males, 3 females, 1 juv.) and 25 paratypes in alcohol in MNHN.

Non-type material. 1 male on slide, 7 specimens in alcohol. South Africa: Western Cape, Stellenbosch, Jonkershoek Nature Reserve., Sosys trail, 12/03/2008, forest litter, Berlese extraction, Louis Deharveng and Anne Bedos leg (SAF-071) — 1 juvenile and 2 females on slides, ibid, Jonkershoek Nature Reserve, Sosys trail, 12/08/2010, litter, Charlene Janion leg (RSA10_JNK026 and RSA10_JNK032, 33°59.758'S, 18°57.156'E) — 1 male, 1 female and 1 juvenile on slides, about 130 in alcohol, ibid, Fish Hoek, Kalk Bay, Echo Valley forest, 05/11/2010, decaying wood of yellowwood, Berlese extraction, Louis Deharveng and Anne Bedos leg (SAF-196).

Description. Length 0.82 – 1.1 mm (males) and 0.75 – 0.85 mm (females). Colour white in alcohol, yellow alive (SAF-196 sample). Eyes 2+2 ommatidia, unpigmented, small (diameter about 1.5-1.8 times that of Ocm socket, Fig. 3A). Habitus similar to *Paleonura* (Fig. 2A). No cryptopygy. Secondary granules rather large (the size of a mesochaeta socket). Dorsal tubercles visible but poorly delimited except on Abd. V-VI, indicated by secondary granules enlarged and irregularly arranged, without clearly developed tertiary granules. No reticulations. No plurichaetosis. Most ordinary dorsal chaetae are macrochaetae of similar length and morphology, basally swollen, straight, cylindrical, long, thick, covered in their 2/3 distal of numerous minute scales, distally sheathed, rounded apically (Figs 2A, 3A, B, C). Some dorsal mesochaetae shorter, bent, acuminate, smooth or weakly rugose on the lateral area of head, on tubercles L of tergites and on Abd. VI. No dorsal microchaetae. S-chaetae thin, 2/3 as long as or slightly shorter than closest macrochaeta (Figs 2A, 3B).

Ant. I with 7 chaetae, Ant. II with 11 chaetae, Ant. III with 16 or 17 chaetae (chaetae d4 and d5 or only d4 absent). Ant. IV organite as a short thick rod; apical bulb simple, low and fused to Ant. IV tip (Fig. 2B). Buccal cone moderately elongated. Maxilla styliform, mandible thin and bidentate with distal tooth subdivided in 2 or 3 minute cilia. Labrum elongate, rounded apically, with ventral sclerifications arc-like. Labral formula 0/2,4. Labium with 4 basal, 3 distal and 3 lateral chaetae, and 2 minute sphaerical x papillae (as in *E. barrai* **sp. n.**, Fig. 5B).

Head chaetotaxy as in Table 1A and Fig. 2A. Head with 6 chaetal groups: CL, 2 (½ Af + Oc), (2 Di, 2 De), 2 (DL, L, So). Central area with macrochaeta B, F, G, Ocm and Ocp. Macrochaeta Ocm internal to ocular line, equally distant to omma or slightly closer to anterior ommatidia; Ocp macrochaeta internal to and at level of posterior omma; Oca absent (Fig. 3A). Posterior area with a very faint tubercle and only 2+2 macrochaetae (Di1 and De1). Five chaetae Vi ventrally on head (Vi5 absent).

Tergite chaetotaxy as in Table 1B and Fig. 2A. Chaeta Di absent on Th. I. Tubercles De and DL separate on Abd. IV. Tubercle L of Abd. IV shift ahead tubercle line Di-De-DL of the tergite. Tubercles Di, De and DL fused on Abd. V on each side of axis. Tubercle Di of Abd. V with Di1 macrochaeta, Di2 and Di3 absent. Abd. VI not or hardly bilobed, with strong secondary granules, present even on the axis. S-chaetotaxic formula: 2+ms, 2/11111. Ventral chaetotaxy similar to that of *E. barrai* **sp. n.**, except the furcal rest in some specimens (Fig. 4C). Secondary sexual characters well developed in the adult male consists of chaetae Ag1 and Ag2 of Abd. V strongly thickened and serrated (Figs 2E, 3F), and chaetae of furcal rest, some Ve of Abd. IV (Fig. 3D), sometimes Ag3 of Abd. V (Fig. 3F), and 3+3 Ve of Abd. VI serrated but less strongly. In a male juvenile from Jonkershoek, chaetae Ag1 were bifid (Fig. 3E).

Microchaetae of furcal rest smaller than secondary granules, often unconspicuous (Fig. 2D). Leg chaetotaxy given in Table 1C. Tita without chaeta M and with chaetae B4-B5 short, not longer than other long chaetae of Tita (Fig. 2C). Claw untoothed, not striated in its basal part, and devoid of secondary granulation.

Derivatio nominis. The species name refers to its reduced chaetotaxy of dorso-internal tubercles of tergotes, which bear only one chaeta from Th. II to Abd. IV (2 or 3 in other species of the genus).

Ecology. All known localities of *Ectonura monochaeta* **sp. n.** belong to the Southern Afrotemperate Forest vegetation type. The species is common in this habitat, typically found in the Western Cape, but absent in shrub formations of the fynbos. The distribution ranges from Table Mountain National Park to Jonkershoek Nature Reserve, Stellenbosch. The species co-occurs with another undescribed species of *Ectonura*.

Discussion. The new species *Ectonura monochaeta* is uniquely identifiable in the genus by the lateral shift of dorso-internal chaetae on Abd. V and their integration in the tubercles (De+DL). Such a lateral shift is only know in *Ectonura paralata* Deharveng, Weiner & Najt, 1997 from New Caledonia, but less marked and without integration of Di chaetae in (De+DL). By other chaetotaxic characters (Di2 and De2 present on head and on tergites of Th. II-Abd. IV; D, E, OcA present on head) and tubercle arrangement (tubercle Di not developed, others as large flat plates), *Ectonura paralata* is however only remotely related to our species. *E. monochaeta* is also distinct from other species of the genus *Ectonura* by the strong reduction of its chaetotaxy: absence of several chaetae on head (A, O, C, D, E, Oca), absence of Di2, De2 and DL2 on tergites, only 2+2 dorsal chaetae on Th. I, and only 6+6 chaetae on Abd. VI.

The lateral shift of Di on Abd. V is one of the characteristic feature of two genera, the monotypic genus *Zelandanura* Deharveng & Wise, 1991 from Campbell Island and *Pronura* Delamare Debouteville, 1953 which is highly diversified in Africa and in Asia. *Zelandanura* differs from *Ectonura* by the fusion in one plate of all tubercles of the central area of head, and by the fusion of Di tubercles on the axis on Abd. IV. Contrary to *Ectonura*, chaetae of the central area of head are not separated in two groups on both side of the axis in *Pronura*.

Ectonura barrai **sp. n.**

Figs 4-6, Table 2.

Type material. Holotype male on slide. South Africa: Western Cape, Grootvadersbosch Nature Reserve, Heidelberg, 24/08/2010, Southern Afrotemperate Forest vegetation, in litter, extraction on Berlese funnel, Charlene Janion leg (RSA10_GVB009, 33°59.167’S, 20°48.639’E).

1 male paratype on slide, same data as holotype — 2 paratypes on slides (1 male, 2 juveniles) and 5 paratypes in alcohol, ibid, Grootvadersbosch Nature Reserve, Heidelberg, 24/08/2010, same habitat, extraction on Berlese funnel, Charlene Janion leg (RSA10_GVB008, 33°58.964’S, 20°48.524'E)

Type deposition. Holotype and 4 paratypes (1 male and 1 juvenile on slides, 2 in alcohol) in IM; 5 paratypes (1 male and 1 juvenile on slides, 3 in alcohol) in MNHN.

Description. Length 1.1-1.3 mm (males). Colour white in alcohol. Eyes 2+2, unpigmented, rather large (diameter about 3 times that of Ocm socket, Fig. 5A). Habitus similar to *Paleonura* (Fig. 4A). No cryptopygy. Secondary granules rather large (the size of a mesochaeta socket). Dorsal tubercles not clearly delimited, only indicated by secondary granules irregularly arranged, without tertiary granules. No reticulations. No plurichaetosis. Ordinary dorsal chaetae differentiated in macrochaetae, mesochaetae and microchaetae (Figs 4A, 6). Dorsal macrochaetae basally swollen, straight or slightly bent, subcylindrical, long, moderately thick, with minute scales sparsed apparently unilaterally, in their distal half, distally sheathed, rounded apically (Figs 5C, D, 6). Dorsal mesochaetae shorter, acuminate to blunt, smooth or weakly rugose. Dorsal microchaetae thin, smooth, less than 1/5 of macrochaetae, present on all tergites (Di2 from Th. II to Abd. V, De3 on Th. II-III, and De2 on Abd. I-V). S-chaetae thin, smooth, acuminate, 2/3 as long as or slightly shorter than closest macrochaeta (Figs 5C, 6).

Ant. I with 7 chaetae, Ant. II with 11 chaetae, Ant. III with 18 chaetae (chaetae d4 and d5 present). Ant. IV organite as a very short thick rod; apical bulb feebly trilobed, fused to Ant. IV tip (Fig. 4B). Buccal cone moderately elongated. Maxilla styliform, mandible thin and bidentate with distal tooth subdivided in 2 or 3 minute cilia. Labrum elongate, rounded and finely denticulated apically, with ventral sclerifications arc--like distally. Labral formula 0/2,4. Labium with 4 basal, 3 distal and 3 lateral chaetae, and 2 minute sphaerical x papillae (Fig. 5B).

Head chaetotaxy as in Table 2A and Fig. 4A. Head with 9 chaetal groups: CL, 2 (½ Af + Oc), 2 DL, 2 (L, So), 2 (Di, De) on very faint tubercles hardly separated on axis. Central area with A, B, D, F, G, Oca, Ocm and Ocp (alternatively, Oca might be homologous of chaeta E). Macrochaeta Ocm internal to ocular line, equally distant from omma; Ocp macrochaeta internal to and at level of posterior omma Oca antero-internal to Ocm. (Fig. 5A) Five chaetae Vi ventrally on head (Vi5 absent).

Tergite chaetotaxy as in Table 2B and Figs 4A and 6. Chaeta Di present on Th. I. Tubercles De and DL fused on Abd. IV. Tubercle L of Abd. IV slightly shift ahead the tubercle line Di-De-DL of the tergite. Tubercles De and DL fused on Abd. V, separated from Di. Tubercle Di of Abd. V with Di1 macrochaeta, Di2 microchaeta and Di3 absent. Abd. VI not or hardly bilobed, with 1+1 areas of slightly enlarged and irregularly arranged secondary granules. S-chaetotaxic formula: 2+ms, 2/11111. No modified chaetae in male (Figs 4E, 5E).

Microchaetae of furcal rest minute and thick, smaller than secondary granule (Fig. 4D). Leg chaetotaxy given in Table 2C, similar to that of *E. monochaeta* **sp. n.** (Fig. 2C). Tita without chaeta M and with chaetae B4-B5 short, not longer than other long chaetae of Tita. Claw untoothed, not striated in its basal part, and devoid of secondary granulation.

Derivatio nominis. This species is named in honour of Jean-Auguste Barra, for his important contribution to the knowledge of South African Collembola.

Ecology. This species was collected in the yellowwood forest leaf litter of Grootvadersbosch Nature Reserve. This is a remnant forest of the larger Tsitsikamma Forest Reserve situated 300 km to the south. The forest consists of indigenous trees such as yellowwood, ironwood and stinkwood.

Discussion. *Ectonura barrai* **sp. n.** is similar to *E. natalensis* in its relatively complete chaetotaxy, but different in several details of chaetal arrangement. Based on the redescription of Coates (1968), *E. natalensis* has a more reduced chaetotaxy than *E. barrai* **sp. n.**: absence of meso/microchaetae D, Di2 and De2 on head, absence of De2 on Th. I, absence of De3 and DL3 on Th. II-III, absence of Di2 on Abd IV-V. Conversely, chaetae Di2, De2 and DL2 on Abd. I-III of *E. natalensis* are much larger than homologous chaetae of *E. barrai* **sp. n.** (macrochaetae or large mesochaetae versus short mesochaetae). Chaetal groups De and DL of Abd. IV are separate in *E. natalensis* versus fused in *E. barrai* **sp. n.**, and chaetal groups Di of Abd. V are fused on axis in *E. natalensis* versus separate in *E. barrai* **sp. n.**. The unusual arrangement of S-chaetae on Ant. IV figured by Coates (1968) is probably an erroneous interpretation, and not considered here as a valid differential character.

Scope of contribution of the candidate

Drawings were done by the candidate, photos by Dr. L. Deharveng. Writing and species descriptions were done by the candidate following advice from Dr. L. Deharveng.

References

Barra, J.A. (1994) Nouveaux Collemboles Poduromorphes de la Province du Natal (Rép. Sud Africaine) (Insecta : Collembola). *Journal of African Zoology* **108**, 181-189.

Cassagnau, P. (1991) *Camerounura* n.g., un Collembole Neanurinae endémique du Mount Cameroun. *Revue d'Ecologie et de Biologie du Sol* **28**, 221-224.

Cassagnau, P. (1996) Collemboles Paleonurini primitifs d'Afrique et de Madagascar. *Annales de la Société entomologique de France* **32**, 121-161.

Cassagnau, P. (2000) Sur quelques Paleonurini d'Afrique Orientale (Collembola: Neanurinae). *Annales de la Société entomologique de France* **36**, 143-155.

Cassagnau, P. and Oliveira, E.P. (1990) Les Collemboles Neanurinae d'Amérique du Sud. *Bulletin de la Société d'Histoire naturelle de Toulouse* **126**, 19-23.

Coates, T.J. (1968) The Collembola from South Africa – I : The Genus *Neanura*. *Journal of the Entomological Society of Southern Africa* **31,** 185-195.

Deharveng, L. (1983) Morphologie évolutive des Collemboles Neanurinae, en particulier de la lignée néanurienne. *Travaux du Laboratoire d'Écobiologie des Arthropodes édaphiques, Toulouse* **4**, 1–63.

Deharveng, L. and Bedos, A. (2002) Nouveaux *Ectonura* de Nouvelle-Calédonie (Collemboles: Neanuridae). In: Zoologia Neocaledonica 5. Systématique et endémisme en Nouvelle-Calédonie. *Mémoires du Muséum national d'Histoire naturelle de Paris* **187**, 91-102.

Gisin, H. (1950) Notes sur les Collemboles avec une espèce, un nom et trois synonymes nouveaux. *Bulletin de la Société Entomologique Suisse* **XXII**, 2.

Greenslade, P. and Deharveng, L. (1991) *Phradmon*, a new genus of Paleonurini (Collembola: Neanuridae) from Australia, with a key to the genera from southern regions and notes on *Pronura*. *Invertebrate Systematics* **5,** 837-854.

Smolis, A. (2008) Redescription of four Polish *Endonura* Cassagnau, 1979 (Collembola, Neanuridae, Neanurinae), with a nomenclature of the ventral chaetae of antennae. *Zootaxa* **1858**, 9-36.

Weiner, W.M. and Najt, J. (1998) Collembola (Entognatha) from East Africa. *European Journal of Entomology* **95,** 217-237.

Womersley, H. (1934) On some Collembola-Arthropleona from South Africa and Southern Rhodesia. *Annals of the South African Museum* **30,** 441-475.

Tables

Table 1. Chaetotaxy of *Ectonura monochaeta* **sp. n. A-Cephalic chaetotaxy**

Group of chaetae	**Tubercle**	**Number of chaetae**	**Type of chaetae**	**Chaetae**
CL	(-)	2 2	M me	F G
1/2Af+Oc	(+)	3	M	B, Ocm, Ocp
2Di, 2De	(+)	2+2	M	Di1, De1
DL, L, So	(-)	5	M	DL1,DL5,L1,L4,So1
		4	me	So3 to 6

B-Tergite chaetotaxy

	Di	**De**	**DL**	**L**
Th. I	-	1	1	-
Th. II	1	1+S	1+S+ms	3
Th. III	1	1+S	1+S	3
Abd. I	1	1+S	1	2
Abd. II	1	1+S	1	2
Abd. III	1	1+S	1	2
Abd. IV	1	1+S	1	5
Abd. V	3+S			2
Abd. VI	6*			

*the ventralmost pair of chaetae is replaced by a unique uneven chaeta in some specimens

Table 1 (continued)

C-Leg chaetotaxy

	Scx2	**Cx**	**Tr**	**Fe**	**Tita**
Leg I	0	3	6	13	18
Leg II	2	7	6	12	18
Leg III	2	8	6	11	17

D-Sternite chaetotaxy

Abd. I	VT: 4	
Abd. II	Ve: 4	(Ve1 present)
Abd. III	Ve: 3	Fu: 3-5me+3mi
Abd. IV	Ve: 7	VL: 4
Abd. V	Ag: 3	VL: 1, with L
Abd. VI	Ve: 12-13	An: 2 mi

Table 2. Chaetotaxy of *Ectonura barrai* **sp. n.**

A-Cephalic chaetotaxy

Group of chaetae	Tubercle	Number of chaetae	Type of chaetae	Chaetae
CL	(-)	2 2	M Me	F G
1/2Af+Oc	(+)	4 2	M Me	A, B, Ocm, Ocp D, Oca
Di, De	(+)	2 2	M Mi	Di1, De1 Di2, De2
DL	(+)	2 2 1	M me mi	DL1, DL5 DL3, DL4 DL2
L, So	(-)	3 5	M me	L1,L4,So1 L2, So3 to 6

B-Tergite chaetotaxy

	Di	De	DL	L
Th. I	1	2	1	-
Th. II	2-3	3+S	3+S+ms	3
Th. III	2-3	3+S	3+S	3
Abd. I	2	2+S	2	3
Abd. II	2	2+S	2	3
Abd. III	2	2+S	2	3-4
Abd. IV	2	4+S		6
Abd. V	2	4+S		3
Abd. VI	7			

Table 2 (continued)

C-Leg chaetotaxy

	Scx2	**Cx**	**Tr**	**Fe**	**Tita**
Leg I	0	3	6	13	18
Leg II	2	7	6	12	18
Leg III	2	8	6	11	17

D-Sternite chaetotaxy

Abd. I	VT: 4	
Abd. II	Ve: 4	(Ve1 present)
Abd. III	Ve: 3	Fu: 4me+4mi
Abd. IV	Ve: 7	VL: 4
Abd. V	Ag: 3	VL: 1, with L
Abd. VI	Ve: 12-13	An: 2 mi*

* those of upper valve shift close to the chaetae of Abd. VI

Figures

Fig. 1: Distribution of Neanurinae previously recorded from South Africa (open symbols) and the two new species described here (closed symbols). Map produced by Vernon Visser.

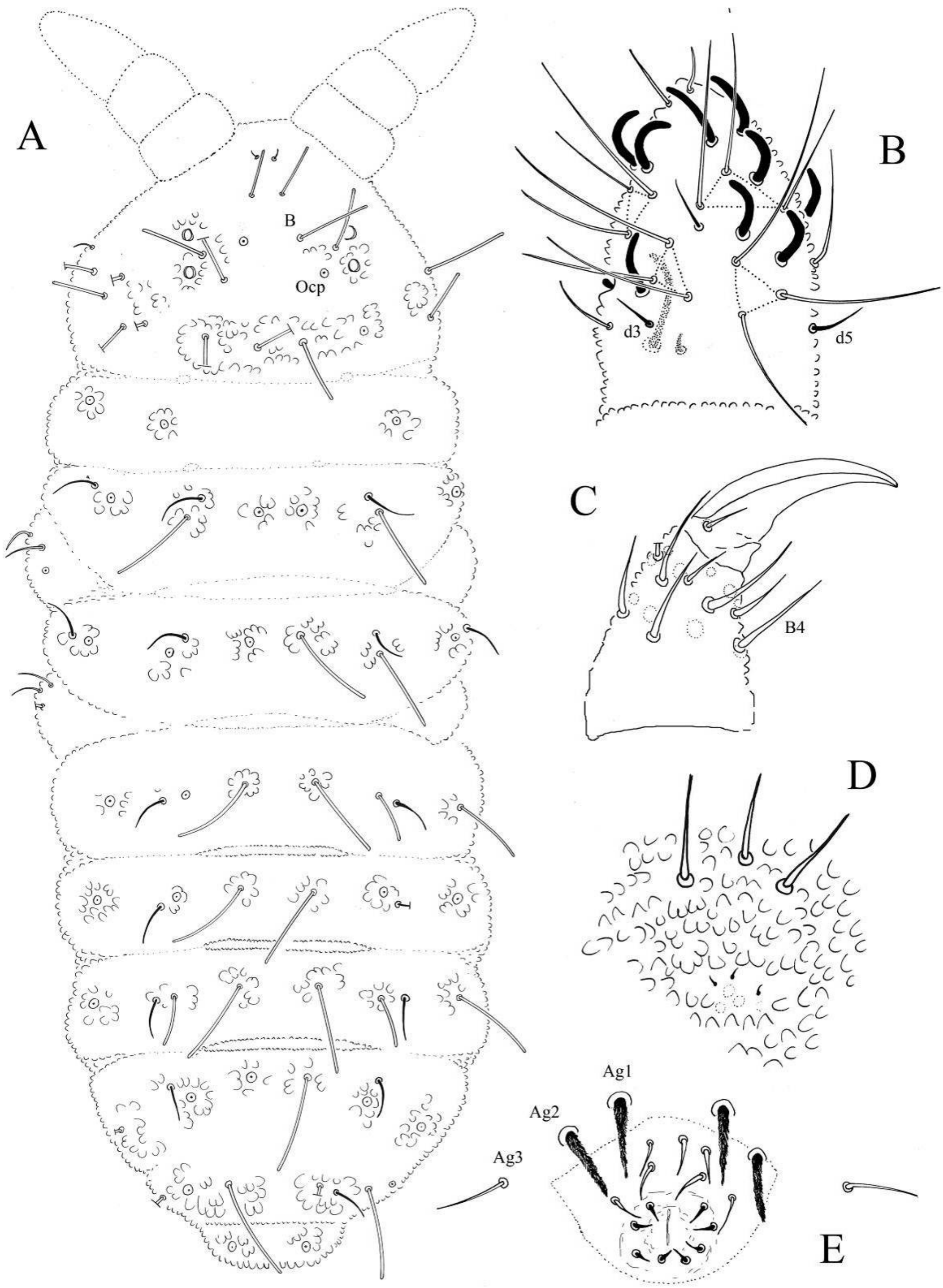


Fig. 2: *Ectonura monochaeta* **sp. n.**; **A,** dorsal chaetotaxy; **B**, Ant. III-IV dorsal side; **C,** tibiotarsus and praetarsus of leg I; **D,** furcal rest; **E,** male genital area. Drawings: C. Janion.

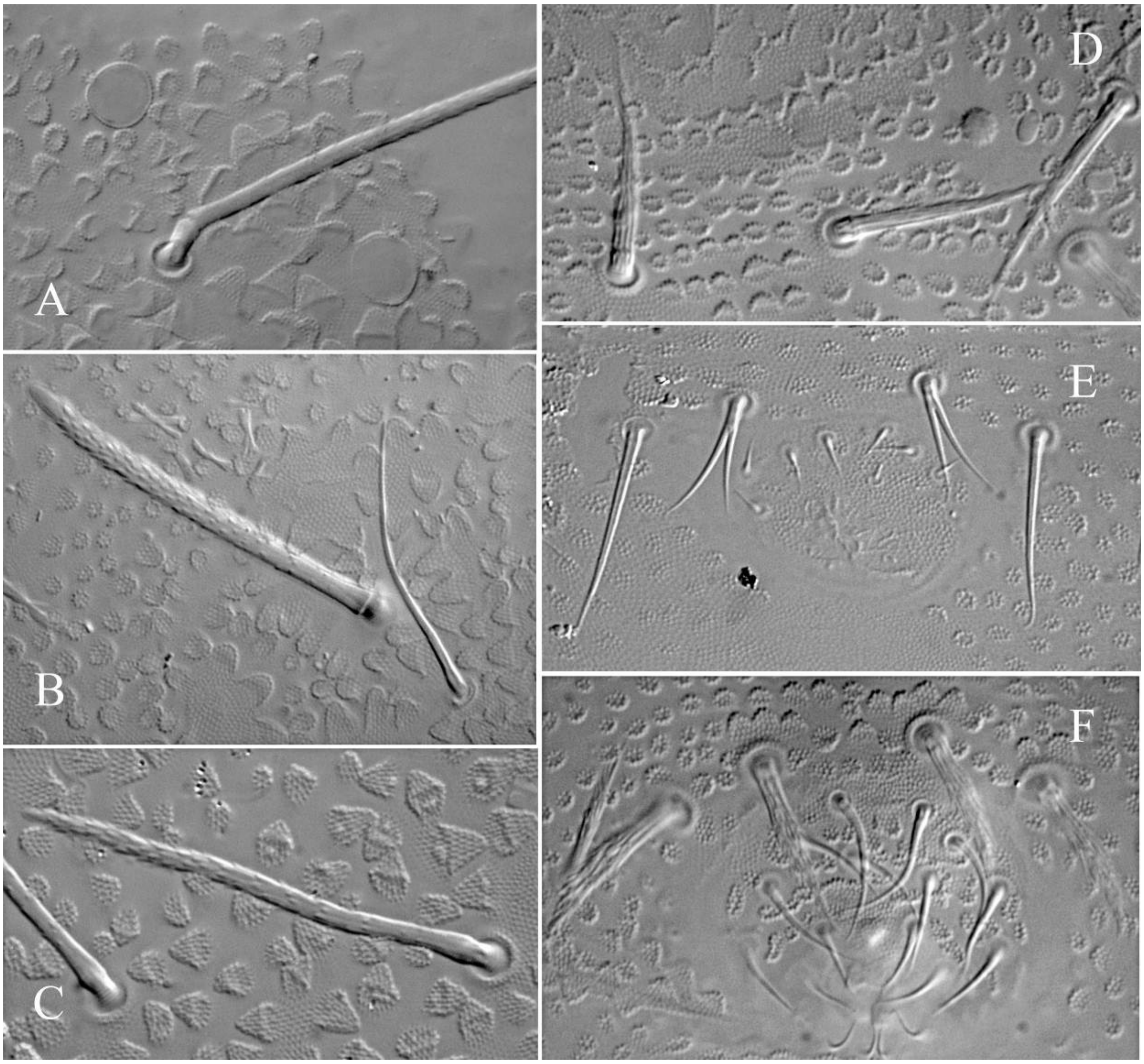


Fig 3: *Ectonura monochaeta* **sp. n.**; **A**, Ocular plate with macrochaeta Ocm; **B**, macrochaeta De1 on Th. II; **C**, chaeta B on head; **D**, chaetae Ve posterior of Abd. IV in a paratype male adult; **E**, genital plate of a male juvenile from Jonkershoek; **F**, genital plate of a male adult. Photo: L. Deharveng.

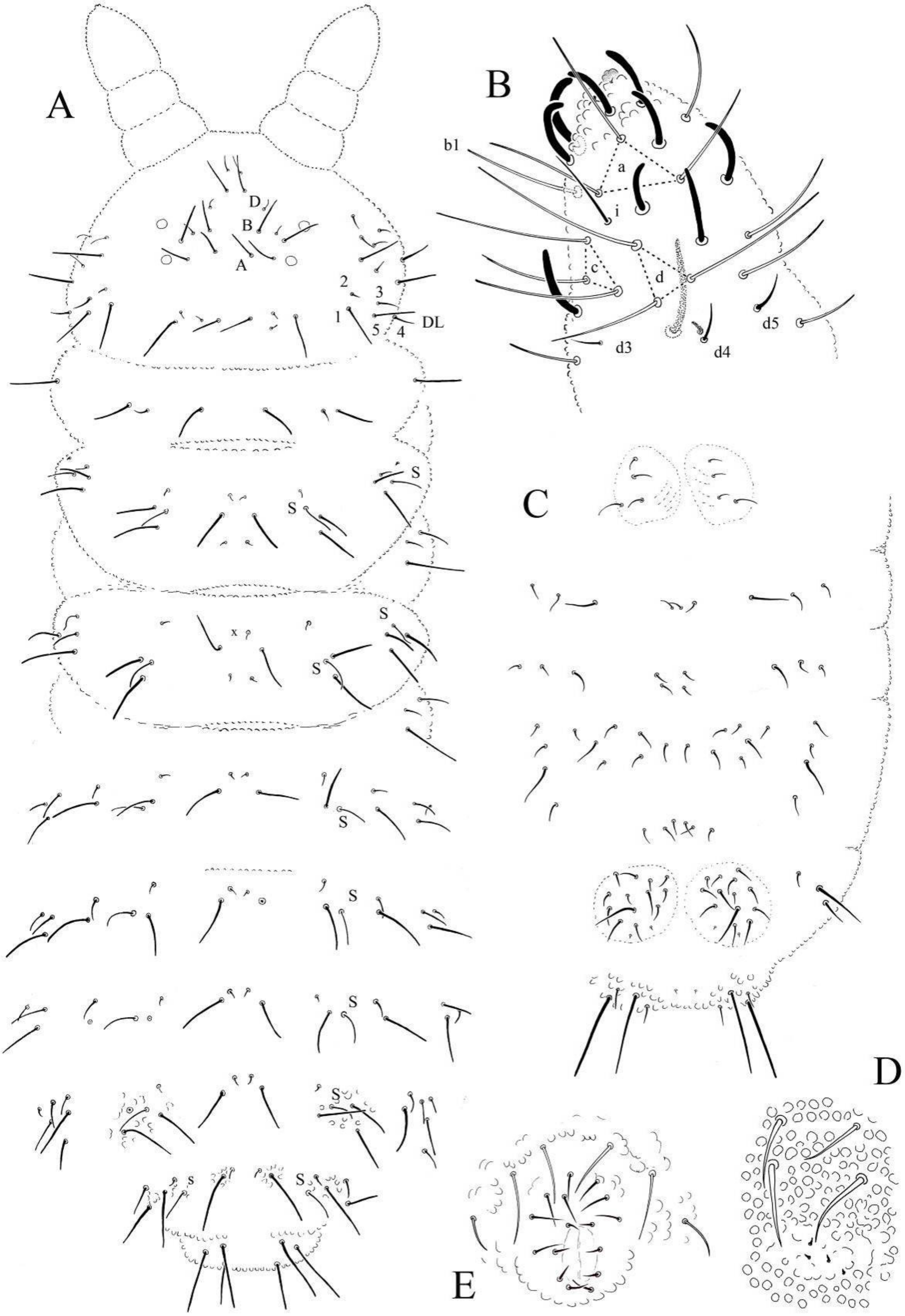


Fig. 4: *Ectonura barrai* **sp. n.**; **A**, dorsal chaetotaxy (tubercles not represented except on Abd. IV-V; x, chaeta Di2 absent unilaterally on Th. III); **B,** Ant. III-IV dorsal side; **C**, ventral chaetotaxy of abdomen; **D**, Furcal rest; **E**, male genital plate. Drawings: C. Janion.

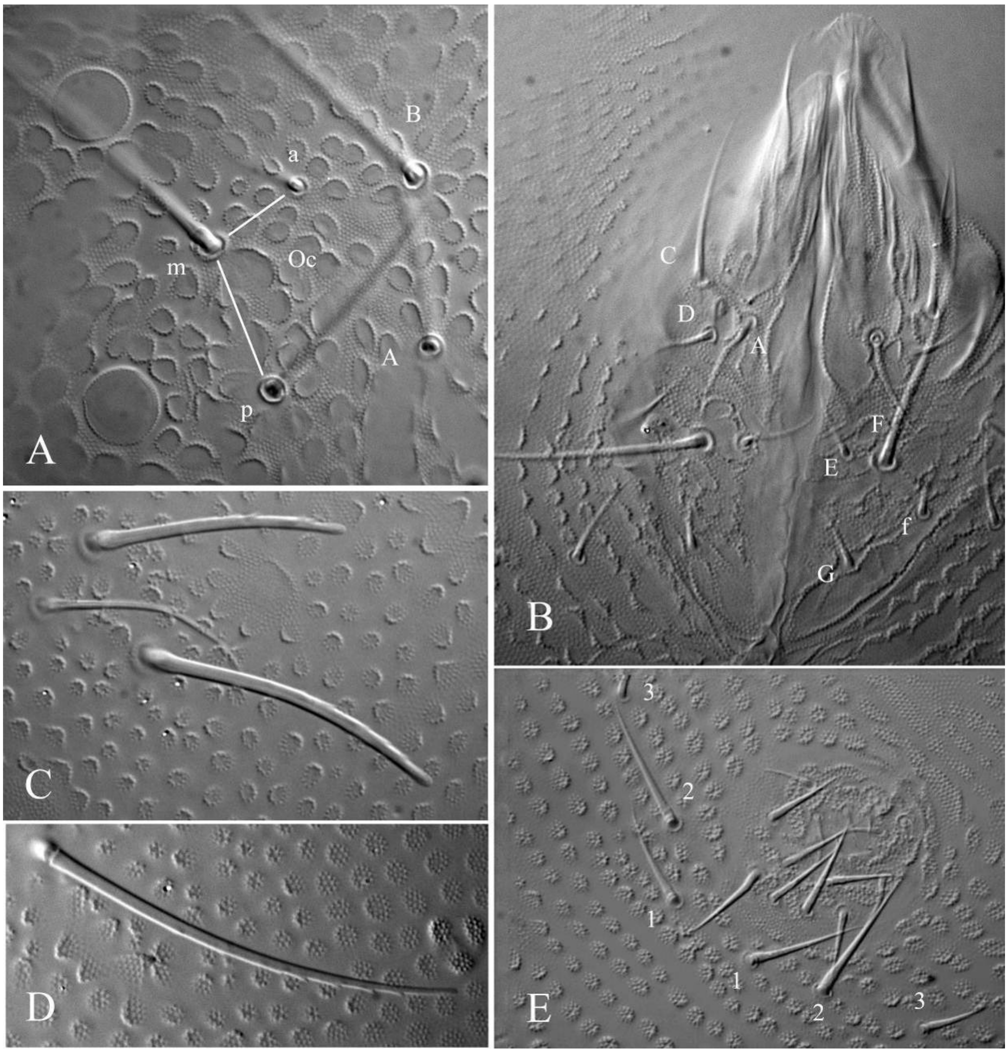


Fig 5: *Ectonura barrai* **sp. n.**; **A**, ocular plate; **B,** Labium; **C**, chaetal group De on Th. III (without the De3 microchaeta); **D**, macrochaeta DL on Abd. I; **E**, male genital plate. Photo: L. Deharveng.

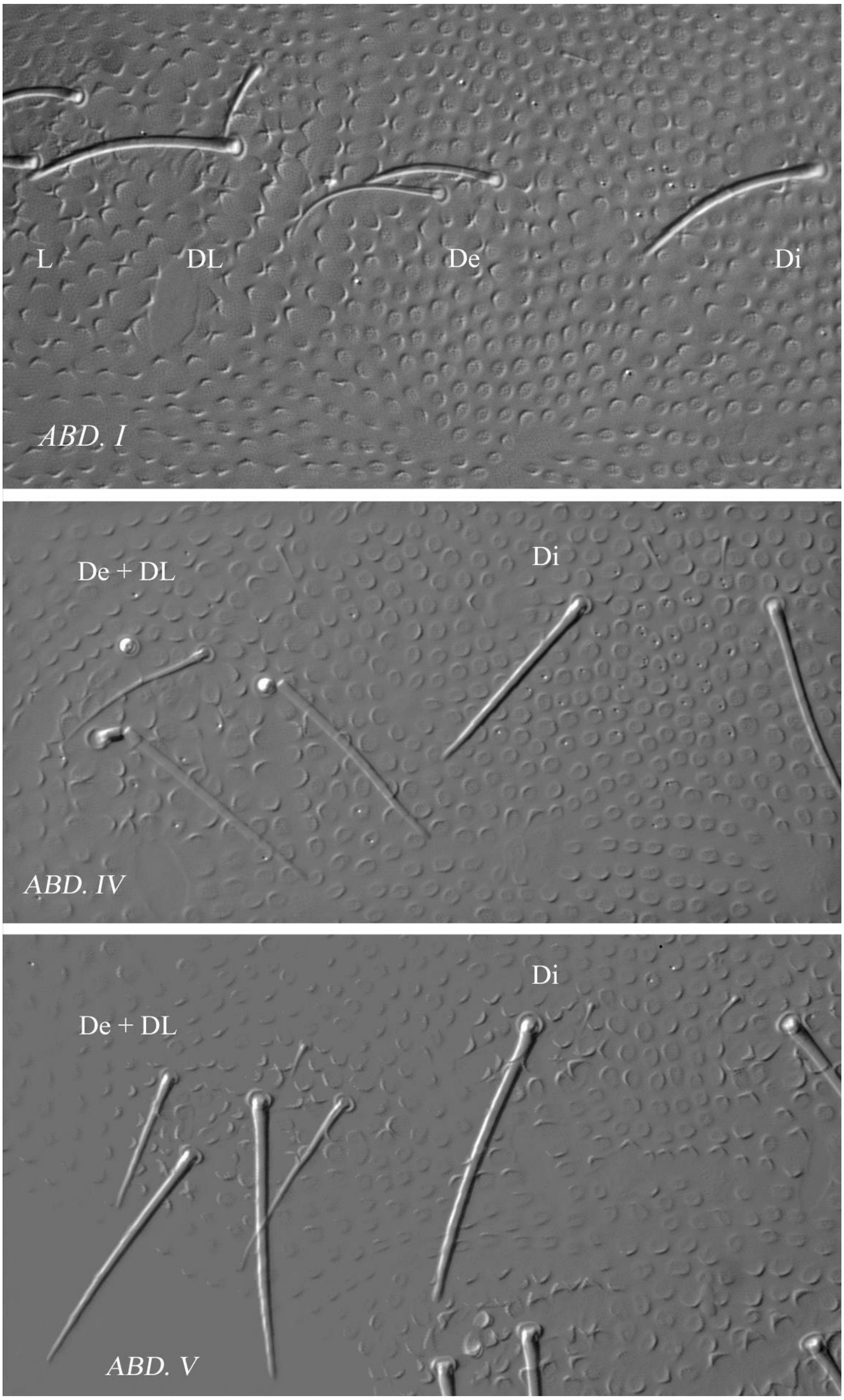
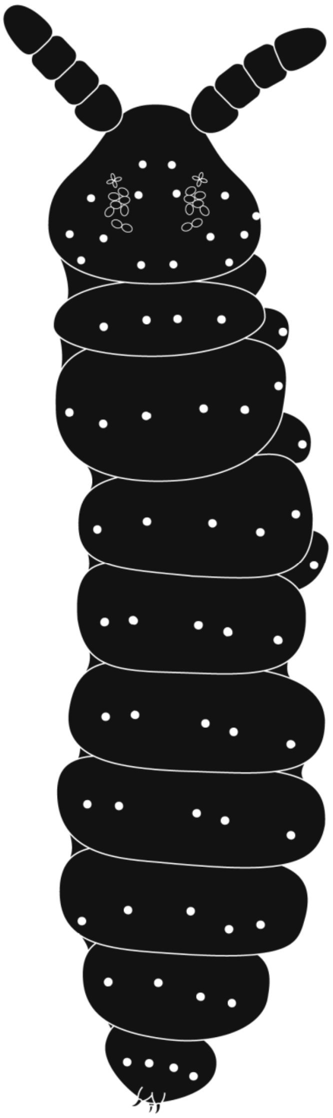


Fig. 6: *Ectonura barrai* **sp. n.**; chaetal groups and faint tubercles Di, De and DL on Abd I, Abd. IV and Abd. V. Photo: L. Deharveng.

Chapter 4

A new species and first record

of the genus *Triacanthella* Schäffer, 1897 (Collembola, Poduromorpha, Hypogastruridae) for Africa



*Published as: Janion, C., D'Haese, C. and Deharveng, L. (2012) A new species and first record of the genus *Triacanthella* Schäffer, 1897 (Collembola, Poduromorpha, Hypogastruridae) for Africa. *Zookeys* **163**, 57-68.

Introduction

The Cape Floristic Region in Western Cape Province of South Africa is the smallest Floral Kingdom in the world. Although its extraordinary rich flora has been well documented (Rebelo et al. 2006), studies have shown that its arthropods are not well known (Pryke & Samways 2008). Recent and extensive sampling of the Collembolan fauna of this region, undertaken within a bilateral project between South Africa and France, provided a wealth of new taxa in all groups (Janion et al. 2011). One of the most interesting discoveries was that of a new species of *Triacanthella*, a genus unrecorded from Africa so far. Here we provide the description of this new South African species along with its biogeographical considerations.

The genus *Triacanthella* is phyletically isolated among Hypogastruridae both from a morphological and a molecular point of view (D'Haese 2002, 2003a, 2003b, Greenslade et al. 2011). It contains 22 species with an intriguing distribution, reflecting a complex and probably ancient history: six including the generotype are in Europe and Asia, eight species in Australia and New-Zealand, seven species in South America and one species in North America. Almost all species are endemic or micro-endemic and restricted to narrow ecological niches (Salmon 1941, de Izarra 1971). They mostly occur in epigean habitats, from warm littoral habitats to permanently cold habitats of high Mediterranean mountains and humid and fresh lowland habitats in southern Australia and New-Zealand. The species *T. perfecta* Denis, 1926 has been found once in a cave in southern France, but its normal habitat is forest litter (Arbea & Jordana 1991). Christiansen and Bellinger (1980) also recorded *T. copelandi* Wray, 1963 once from a cave, but without mentioning if it was also found in the area outside the cave. The presence of a *Triacanthella* species in the guano of an African cave is therefore a surprising and important discovery.

Materials and methods

The terminology used in the text follows D'Haese (2003a, b), and Fjellberg (1984, 1999) for mouthparts. Abbreviations used: Type deposit – **IM**, Iziko Museum (Cape Town, South Africa); **MNHN**, Museum National d'Histoire Naturelle (Paris, France). Abbreviations used in description – **AIIIO**, organite of Ant. III; **Abd. I-VI**, abdominal segments, **Ant. I-IV**, antennal segments; **ms**, S-microchaeta; **s**, s-chaeta; **Th. I-III**, thoracic segments; **Md**, dorsal macrochaeta; **Mdl,** dorso-lateral macrochaeta; **hr**, anal valve chaetae.

Identification key to the Southern Hemisphere *Triacanthella* species.

0 Sixth abdominal tergum with rosette-shaped tubercles, South America only ………….1

Sixth abdominal tergum without rosette-shaped tubercles ……………………………....5

1 Empodium absent, claw without inner tooth ……………………………………………….2

Empodium present (but rudimentary), claw with two inner teeth…………………………..3

2 Omatidia G similar in size to the other ommatidia, Argentina………………………………………………………..***Triacanthella michaelseni* Schäffer, 1897**

\- Omatidia H and G reduced compared to the other ommatidia, Argentina ………………………………………………………………………………***Triacanthella rosae* Wahlgren, 1906**

3 Posterior anal spine less than half the size of the other two, dentes without apical lobe, Chile……………………………………………………… ***Triacanthella vogeli* Weiner & Najt, 1997**

\- Posterior anal spine at least half the size of the other two, dentes with distinct apical lobe……4

4 Macrochaetae long, half tergite macrochaetal chaetotaxy = 7/233/4444, Chile and Argentina ……………………………………………***Triacanthella andina* Cassagnau & Rapoport, 1962**

\- Macrochaetae short, half tergite macrochaetal chaetotaxy = 8/244/3333, Argentina ………………………………………………………………………………***Triacanthella najtae* de Izarra 1971**

5 Posterior anal spine at least half the size of the other two…………………………………. 6

Posterior anal spine less than half the size of the other two ………………………………12

6 Mucro reduced to a small projection (i.e. almost absent) ……………………………………7

\- Mucro well developed ……………………………………………………………………………………8

7 Colour in alcohol pinkish, Campbell Island ……..***Triacanthella sorenseni* Salmon, 1949**

\- Colour in alcohol whitish-yellowish, Campbell Island……………………………………………… ………………………………………………………………………………***Triacanthella alba* Carpenter, 1906**

8 Mucro simple and straight………………………………………………………………………………9

- Mucro not simple with two teeth……………………………………..……………………………….……10

9 All ommatidia equally developed, tibiotarsi with clavate tenent hair, Argentina………………………………………………….………………………***Triacanthella massoudi* Najt, 1973**

- Two ommatidia (G and H) absent, tibiotarsi without clavate tenent hair, Australia………………………………………………………………….***Triacanthella violacea* Womersley, 1939**

10 Macrochaetae simple and smooth, New Zealand …***Triacanthella rubra* Salmon, 1941**

- Macrochaetae serrated or brush-like…………………………………………………….………….11

11 All ommatidia equally developed, apical lobe absent on dentes, New Zealand………………………………………………………………..***Triacanthella purpurea* Salmon, 1943**

- Two ommatidia (G and H) reduced, apical lobe present on dentes, New Zealand…………………………………………………………….***Triacanthella enderbyensis* Salmon, 1949**

12 Two ommatidia (G and H) reduced ……………………………………………………………...13

All ommatidia equally developed …………………………………………………………………….14

13 Dentes reduced, empodium present (but rudimentary), Chile……………………………………………………………………..….***Triacanthella clavata* Willem, 1902**

- Dentes normally developed, empodium absent, New Zealand……………………………………………………………***Triacanthella terrasilvatica* Salmon, 1943**

14 Mucro more complex with two teeth, colour whitish-yellowish in alcohol, claw without inner tooth, New Zealand …………………..***Triacanthella setacea* Salmon, 1941**

- Mucro with a distinct heel, colour pinkish in alcohol, claw with two inner teeth, South Africa ……………………………………………………………… ***Triacanthella madiba* sp. n.**

Species description

Triacanthella madiba sp. n.

Material

Holotype female and 17 paratypes (8 on slide and 9 in alcohol), South Africa: Western Cape, Cape Town, Table Mountain National Park, 10 March 2009, bat guano in Wynberg cave, S33° 59,193, E18°24,160', extracted on Berlese-Tullgren funnel, (SAF-125, Louis Deharveng & Anne Bedos leg). Holotype on slide and 9 paratypes (4 on slides and 4 in alcohol) in Iziko

Museum (Cape Town, South Africa), 8 paratypes in Museum National d'Histoire Naturelle, Paris (4 on slides and 4 in alcohol). Slides were studied under a Leica DM2000 compound microcope with phase contrast and drawings were made using a Leica drawing tube.

Description

Colour orange to pink alive, pinkish in ethanol even after 1.5 years (Fig. 1). Length 1.9 – 2.5 mm. Habitus of Southern Hemisphere *Triacanthella* (Figs 1, 6A).

Dorsal integument ornamentation made of hemispherical and rather coarse secondary granules, with large areas devoid of secondary tubercles on head and tergites (Figs 2-3), symmetrically arranged; most noticeable are the long antero-axial one on head, those associated to classical suture zone of head (Fig. 2), the 1+1 amiboid ones on Th. II-III (Fig. 3A), and the triangular ones between Md and Mdl on Abd. I-III (Figs 3B-C); secondary granules smaller around these areas. Externally to ocular area is a large area where secondary granules are smaller and denser (Fig. 3D). Secondary granules larger along the axial zone (Fig. 3E). No rosette-like arrangement of secondary granules on Abd. VI. Ventral secondary granulation less coarse, more regular. Manubrium with secondary granules arranged in a characteristic linear pattern dorsally (Fig. 3F), and with large areas devoid of secondary granulation ventrally. Pseudopores not seen. Chaetotaxy characterized by a strong heterochaetosis dorsally and a moderate plurichaetosis on most body parts. Chaeta morphology described below, with macrochaetae, mesochaetae and S-chaetae on head and body, and various kinds of chaetae on antennae (Figs 4, 6C). No ordinary microchaetae except on praetarsus and genital plate.

Antennae almost as long as head diagonal. Six kinds of antennal chaetae: i) thickened subcylindrical S-chaetae of medium size (2 on Ant. III and 6 on Ant. IV); (ii) S-microchaetae (3 on Ant. III and 1 on Ant. IV) (Figs 4B-C); (iii) blunt chaetae very similar to the S-chaetae, but longer and usually slightly thinner (on Ant. IV); (iv) acuminate ordinary chaetae of various length, smooth or weakly serrated, 11-12, 13-17 and 26-30 on Ant I-III, a few on Ant. IV (Fig. 4D); (v) thin, straight and smooth truncated chaetae numerous ventrally on Ant. IV (Fig. 4A); (vi) one ventro-distal papillate chaeta. Sensory organ of AIIIO with two short S-chaetae lying in ovoid sockets (S2 and S3, Fig. 4B), two longer guard S-chaetae shorter than nearest mesochaetae (S1 and S4) and one very small dorso-external S-microchaeta (S5); integument granulation significantly coarser between and above S2 and S3 (Fig. 4B). Antennal segment IV with most chaetae as subcylindrical, thickened, blunt S-chaetae, the shortest ones slightly thicker and more bent, including a central group of six; apical bulb trilobed; subapical organite rounded, very small; a short ovoid-elongate S-microchaeta present dorso-externally (Fig. 4C, 6B).

Eight ommatidia on each side of the head, equal in size. Postantennal organ nearly equal in size to one ocelli with 4 subequal vesicles (Fig. 2). Maxilla with a tridentate capitulum, a rounded basal flap and 6 variously fringed or ciliate lamellae (Figs 5C-D). Mandible head with 4 teeth on each side, the basal one slightly smaller on the left than on the right mandible (Figs 5A-B). Labrum chaetotaxy 4/4,5,4; labral chaetae distinctly longer than prelabral chaetae; labrum apical edge with a slight medial indentation; distal part with four irregular longitudinal ridges dorsally, and with subapical asymmetrical combs ventrally (Figs 5E-G); labral apical edge hemmed (Fig. 5G). Labium with 5-6 basomedian chaetae, 7 lateral chaetae, and a labial palp characterized by 7-8 proximal chaetae and a reduced number of distal chaetae (Fig. 5J): only 3 papillae, A,B,D; one ordinary chaeta (possibly e4, but with a socket) and 5 short, thickened, hyaline guards (a1, b1, b2, d2, Fig. 5I), with the fifth one probably the labial process sensu Fjellberg (1999). Maxillary outer lobe with one basal chaeta and a simple palp; sublobal plate small, rounded and devoid of sublobal hairs. Clypeus with 15-16 chaetae (Fig. 5H). Postlabial chaetae 5+5.

Chaetotaxy of tergites illustrated on Fig. 6A. Dorsal clothing plurichaetotic and heterochaetotic, with frequent asymmetries among shortest mesochaetae. Macrochaetae long, bent, and densely ciliated unilaterally on 2/3 to most of their length; mesochaetae, less bent, acuminate, less strongly ciliated to almost smooth; S-chaetae, thin and smooth, shorter than macrochaetae (Figs 4E-G, 6C). Macrochaetae formula per half-tergite: 8/2,3,3/3,3,3,3(4),3. Number of chaetae between macrochaetae Md per half-tergite: 1-2,3-5,3-4/2-3,2-3,(1)-2,3,2-3 with many asymmetries. S-chaetae formula per half-tergite: 0,2,2/1,1,1,1,1; microchaeta ms absent. Abdomen VI chaetotaxy often asymmetrical, with one or two axial short mesochaeta; three anal spines on papillae, the posterior one half the length of the other two which are hook-like (Figs 6G-H).

No ventral chaetae on thoracic sternites. Number of ventral chaetae per half-tergite for Abd. II, III: 7, 13-17; anterior furcal subcoxa with 12-16 chaetae. All ventral chaetae are smooth ordinary chaetae. Lateral anal valves with 3 or 4 hr chaetae; upper anal valve with 7-9 hr chaetae.

Leg chaetotaxy slightly plurichaetotic. Trochanter with 7 chaetae. Tibiotarsi I, II, III with (proximal + distal): 8 + 11, 8 + 11, 7 + 11 acuminate chaetae. No clavate tenent hair. Claw with two inner teeth at about 40% and 65% of claw basis, and 1 + 1 latero-distal teeth, appressed on the integument and difficult to see at about 85% of claw basis (Fig. 6D). Empodial appendage short and pointed, internal to empodial apical tubercle according to figure 6E, 1+1 small praetarsal microchaetae. Ventral tube with 9-11 + 9-11 latero-distal chaetae, and 1-2 chaetae on each side of the sternite of Abd. I. Tenaculum with 3 + 3 teeth. Dens without ventro-apical lobe, bearing 10-15 chaetae dorsally with fine granulation (secondary granules smaller than chaetal sockets); the basal macrochaeta of the dens is about 2.3 the length of the nearest mesochaeta; well developed mucro with a large lamella and a very distinct dorso-basal heel (Figs 6E-F).

Discussion

Triacanthella madiba sp. n. shares numerous characters with *T. vogeli* Weiner & Najt, 1997, described from southern Chile. It differs mainly by the ocelli G and H being equal in size to the other ocelli and the absence of rosette-shape tubercles on Abd. VI. It is also morphologically close to *T. andina* Cassagnau & Rapoport, 1962 from Argentina, but macrochaetae are less numerous on Abd. I-III (333 versus 444 in *T. madiba* sp. n.). In addition, the lamellae of the maxilla are shorter and the papillae bearing the anal spines are not as strong in *T. madiba* sp. n., as in *T. andina*. Overall, these three species are extremely similar morphologically in spite of being very remote geographically. *Triacanthella madiba* sp. n. differs from Australian and New-Zealand species by characters pointed out in the key. An additional important character is the chaetotaxy of the distal part of the labial palp, which is similar to that described for an unidentified species of Australia (Fjellberg 1999), being strongly reduced compared to that of *T. biroi*, Stach 1924 from Europe (Fjellberg 1999).

Distribution and ecology

Triacanthella madiba sp. n. is recorded in bat guano in a cave of Table Mountain National Park. This is the first record of the genus *Triacanthella* in a guano habitat and the first record of the genus for Africa. None of the *Triacanthella* species recorded thus far have been found in tropical regions. They are all restricted to temperate zones, where they occur in a large range of habitats in Europe (from xeric Mediterranean to permanently cold), while they are limited to humid and cool litter or surface soil layers in the southern hemisphere (Australia, New Zealand, Chile and Argentina, Weiner & Najt 1997). Its presence underground in a cool, nutrient rich and permanently humid habitat, and its absence in the remnant forest patches of Table Mountain that we sampled extensively is surprising.

The only subterranean records of the genus *Triacanthella*, include the record of *T. copelandi* in a cave in Tennessee (USA), without additional detail, and a single specimen collected in a small shallow cave of oriental Pyrenees in France, that was described as *T. proxima* Delamare 1951, and later synonymised with *T. perfecta.* In the area around this last cave, *T. perfecta* is actually common in beech forest litter (unpublished observations), and its presence underground as a single specimen is obviously accidental. Conversely, *T. madiba* sp. n. occurred abundantly in the guano microhabitat of Wynberg cave and was not found outside in Table Mountain. The species can therefore be considered troglophilic in this area. Actually, *T. madiba* sp. n. may have been already recorded as *Schaefferia* (*Typhlogastrura*) sp. in Sharratt et al. (2001), collected from guano material during a cave fauna survey in Table Mountain.

Although the labial palp of *T. madiba* sp. n. is similar to the unidentified Australian species (Fjellberg 1999), it also shares some characters with certain South American species, making its placement in the phylogeny based on morphological characters problematic. If the new species is more closely related to the Australian and New-Zealand species, it would follow a classical transantarctic gondwanian pattern (Brundin, 1965, 1966, Sanmartín & Ronquist 2004). Alternatively, it could be that *T. madiba* sp. n. is more closely related to South American species based on the characters pointed out in the key provided. Thus, it could be that *T. madiba* sp. n. is the result of dispersal from South America (e.g. Allwood et al. 2010), associated with a significant shift in its ecological requirements. On-going molecular and morphological studies on this basal genus will hopefully resolve their intriguing biogeographic pattern.

Name derivation.

We dedicate this species to Madiba, former President of South Africa, Nelson Rolihlahla Mandela, who celebrated his 20 years of freedom on 11 February 2010.

Scope of contribution of the candidate

Drawings were done by the candidate, photos by Dr. L. Deharveng. Writing and species description were done by the candidate following advice from Dr. L. Deharveng.

References

Arbea J.I. & Jordana, R. (1991) Colémbolos de Navarra (norte de la Península Ibérica). I. Orden Poduromorpha (Collembola) Publicacíones de Biología de la Universidad de Navarra, *Serie Zoologica* **22**, 1-149.

Allwoood, J., Gleeson, D., Mayer, G., Daniels, S., Beggs, J.R. & Buckley, T.R. (2010) Support for vicariant origins of the New Zealand Onychophora. *Journal of Biogeography* **37,** 669-681.

Brundin, L. (1965) On the real nature of transantarctic relationships. *Evolution* **19,** 496-505.

Brundin, L. (1966) Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kungl. *Svenska Vetenskapsakadem- iens Handlinger, Fjarde Serien*, **11**:472, 30 pp.

Christiansen, K. & Bellinger, P. (1980) *Part I. Poduridae and Hypogastruridae, The Collembola of North America North of Rio Grande*, Grinnell College, Iowa, 386 pp.

de Izarra, D.C. (1971) Sobre el genero *Triacanthella* Schäffer con descripcion de una nueva especie: *T. najtae* (Insecta, Collembola). *Physis* **30,** 345-350.

D'Haese, C.A. (2002) Were the first springtails semi-aquatic? A phylogenetic approach by means of 28S rDNA and optimization alignment. *Proceedings of the Royal Society of London B* **269,** 1143-1151.

D'Haese, C.A. (2003a) Homology and morphology in Poduromorpha (Hexapoda, Collembola). *European Journal of Entomology* **101,** 385-407.

D'Haese, C.A. (2003b) Morphological appraisal of Collembola phylogeny with special emphasis on Poduromorpha and a test of the aquatic origin hypothesis. *Zoologica Scripta* **32,** 563-586.

Fjellberg, A. (1984) Maxillary structures in Hypogastruridae (Collembola). *Annalesde la Société Royale de Zoologie de Belgique* **114,** 89-99.

Fjellberg, A. (1999) The labial palp in Collembola. *Zoologischer Anzeiger* **237,** 309-330.

Greenslade, P., Stevens, M.I., Torricelli, G. & D'Haese, C.A. (2011) An ancient Antarctic endemic genus restored: morphological and molecular support for *Gomphiocephalus hodgsoni* (Collembola: Hypogastruridae). *Systematic Entomology* **36,** 223-240.

Janion, C., Bedos, A., Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, H.P., Liu, A., Malmström, A., Porco, D. & Chown, S.L. (2011) Springtails diversity in South Africa*.* *South African Journal of Science* **107**, #582, 7 pages.

Pryke, J.S. & Samways, M.J. (2008) Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation* **17,** 3027-3043.

Rebelo, A.G., Boucher, C., Helmem, N., Mucina, L. & Rutherford, M.C. (2006) Fynbos Biome. In: L. Mucina & M.C. Rutherford (Eds) *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, 52-219.

Sanmartín, I. & Ronquist, F. (2004) Southern Hemipshere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* **53**, 216-243.

Salmon, J.T. (1941) The Collembolan Fauna of New Zealand, including a discussion of its distribution and affinities. *Transactions of the Royal Society of New Zealand* **70,** 282-431.

Sharratt, N.J., Picker, M.D. & Samways, M.J. (2000) The invertebrate fauna of the sandstone caves of the Cape Peninsula (South Africa): patterns of endemism and conservation priorities. *Biodiversity and Conservation* **9,** 107-143.

Weiner, W.M. & Naijt, J. (1997) Collembola Poduromorpha from the Magallanes Province (Chile). *Bonner Zoologische Beiträge* **47,** 99-110.

Figures

Fig. 1: *Triacanthella madiba* sp. n., aspect and colour after one year in 95% ethanol. Photo: L. Deharveng.

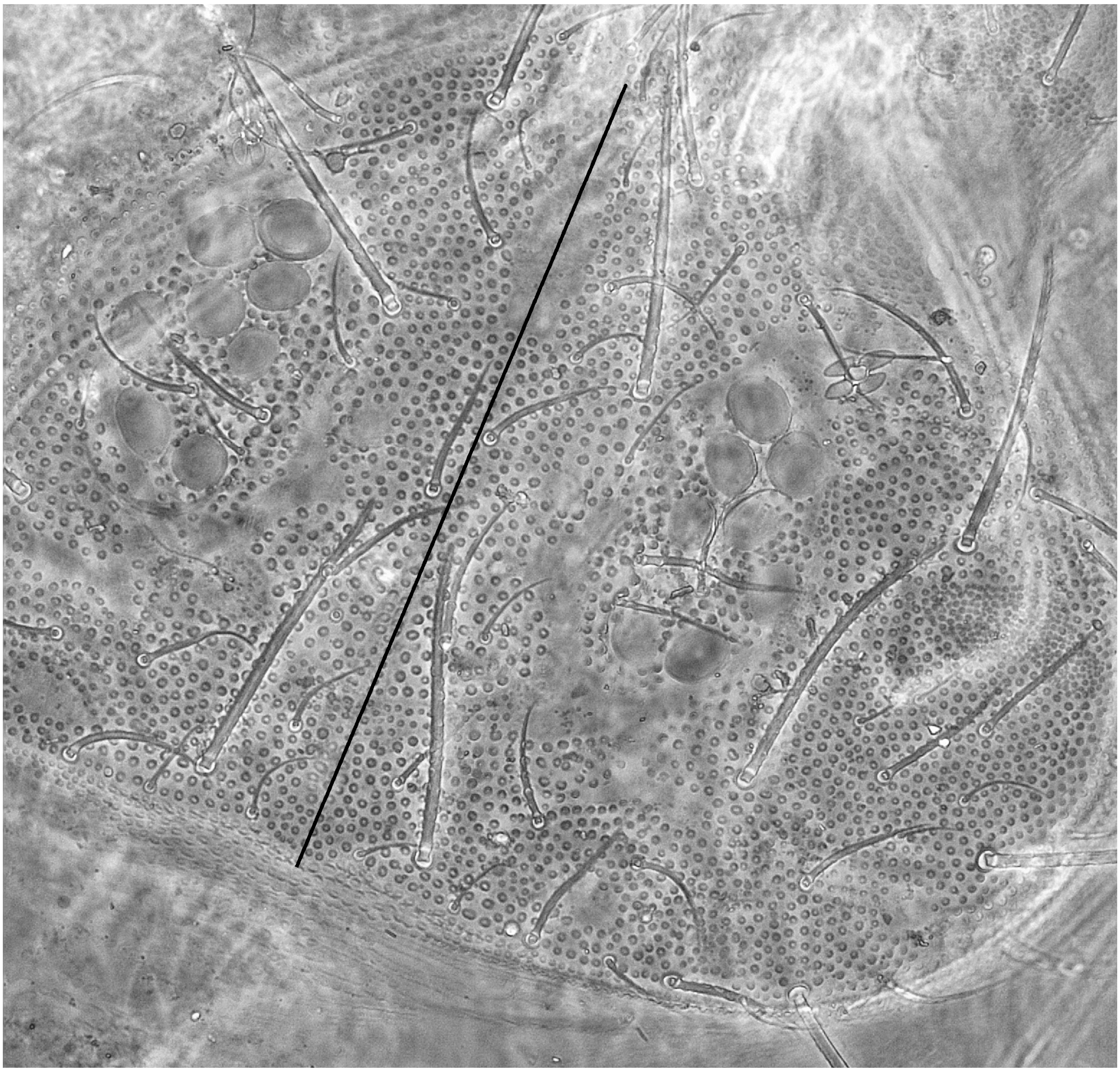


Fig. 2: *Triacanthella madiba* sp. n., dorsal side of head. Photo: C. Janion.

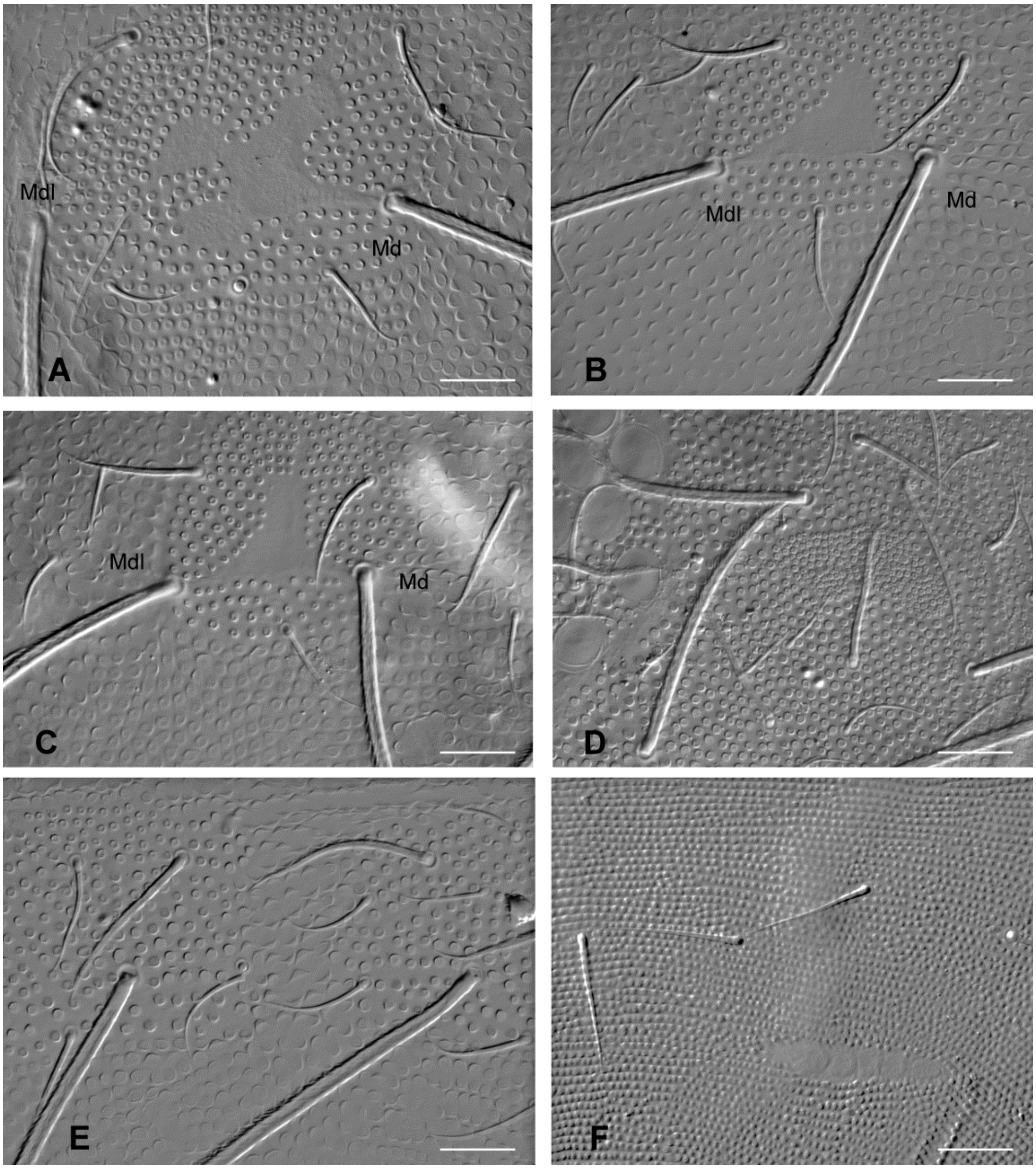


Fig. 3: *Triacanthella madiba* sp. n., details of granulation types on dorsal side of the body. A, amiboid primary granule area on Th. III; B, triangular primary granule area on Abd. III; C, triangular primary granule area on Abd. II, surrounded by smaller secondary granules; D, detail of the lateral plate of smaller secondary granules on head; E, axial area of Abd. V, with larger secondary granules between axial chaetae; F, linear arrangement of secondary granules on the manubrium. Scales: 30 µm. Photo: L. Deharveng.

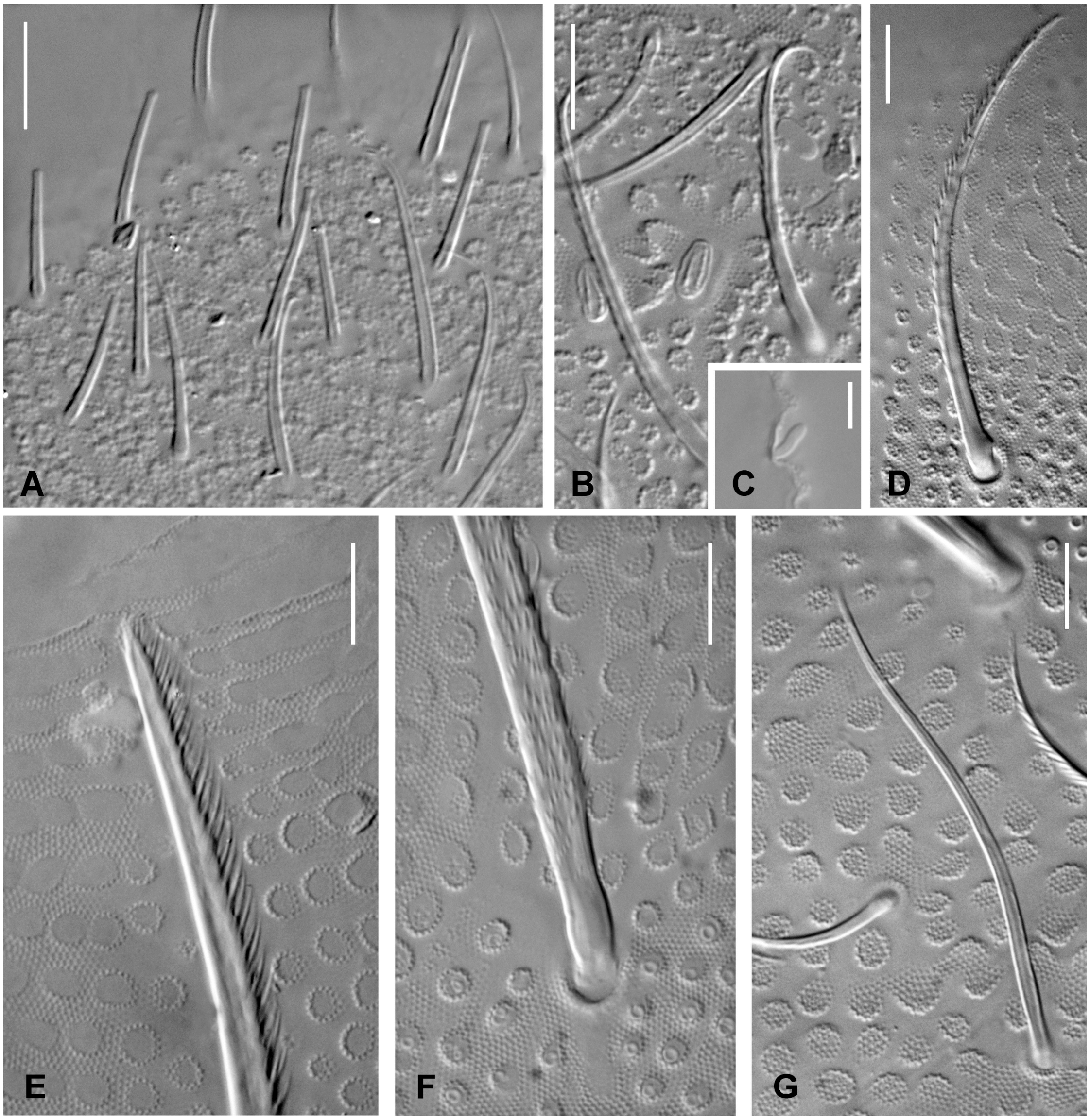


Fig 4: *Triacanthella madiba* sp. nov., types of chaetae. A, truncated chaetae of the ventral side of Ant. IV; B, microchaetae S3 and S4 of AIIIO; C, S-microchaeta of Ant. IV; D, ciliated chaeta of Ant. III; E, distal part of a macrochaeta on Abd. I; F, basal part of a macrochaeta on Abd. III; G, S-chaeta on Abd. I. Scales: 10 µm (A, B, D, E, F, G); 5 µm (C). Photo: L. Deharveng.

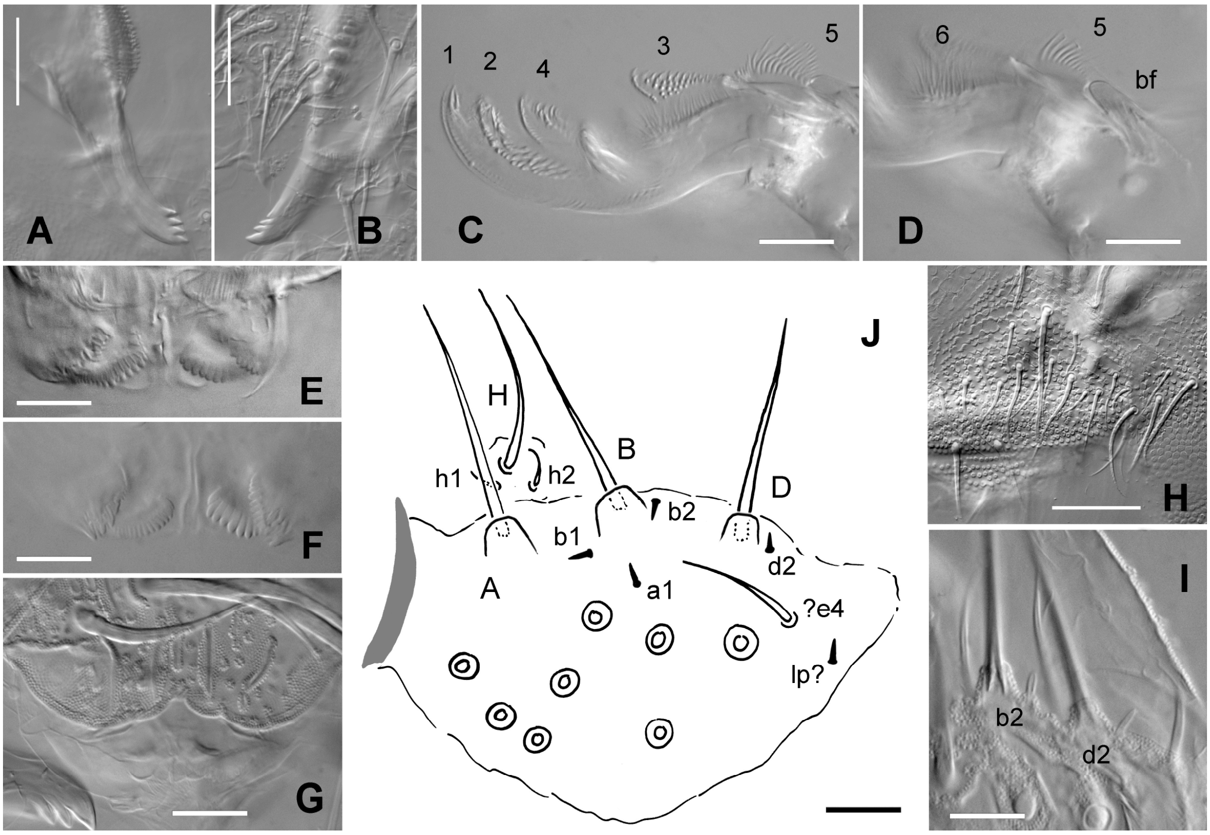


Fig. 5: *Triacanthella madiba* sp. n., mouthparts. A, mandibles, right; B, mandibles, left; C, maxilla head; D, proximal part of maxilla head, with basal flap bf; E, F, ventro-distal part of labrum with combs; G, dorso-distal part of labrum; H, clypeus; I, guards b2 and d2 of labial palp; J, labial palp. Scales: 10 µm. Photo and drawing: L. Deharveng.

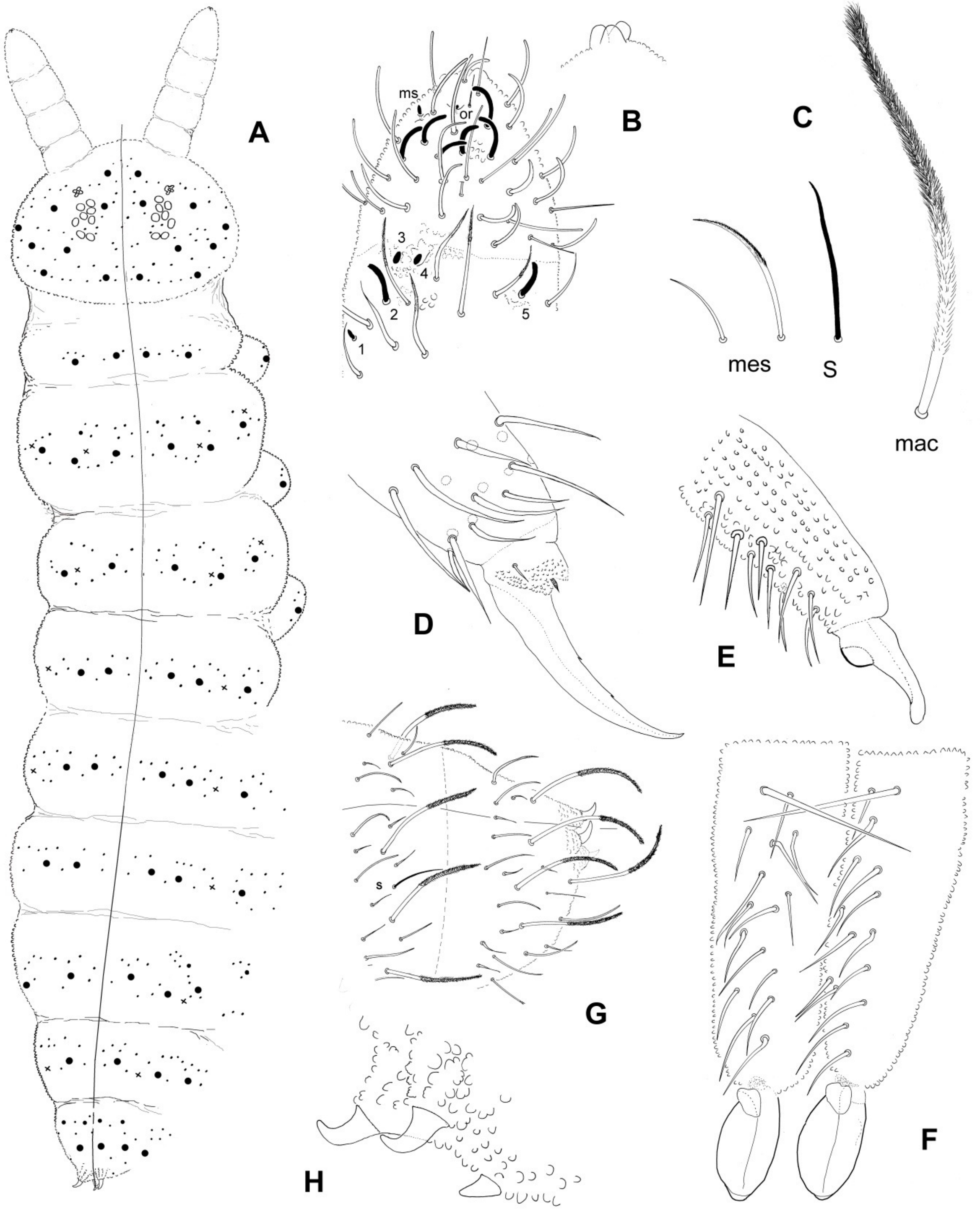
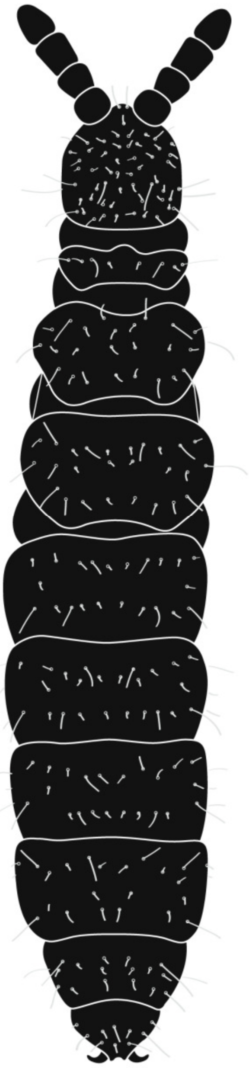


Fig. 6: *Triacanthella madiba* sp. n., A, habitus and chaetae distribution of the dorsal side (x: S-chaetae); B, Ant. III distal and Ant. IV in dorsal view and detail of the apical bulb; C, morphology of dorsal chaetae: macrochaeta (mac), mesochaeta (mes), S-chaeta (s); D, tibiotarsus and claw of leg III; E, mucrodens, lateral view; F, Mucrodens, dorsal view; G, Abd. V-VI tergites; H, anal spines. Drawings: C. Janion (except Fig. 6D by L. Deharveng).

Chapter 5

Synonymy of *Spicatella* Thibaud, 2002

with *Delamarephorura* Weiner & Najt, 1999, with description of two new species (Collembola: Tullbergiidae)



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Introduction

Weiner & Najt (1999) established the genus *Delamarephorura* for *Mesaphorura salti* Delamare-Deboutteville, 1953 from Tanzania, on the basis of a set of morphological features: Abd. VI with a medial process ventrally, double crescentic ridges and two strong spiniform processes dorsally; simple vesicles in the postantennal organ; pseudocelli shape; and pseudocellar formula. A few years later, Thibaud (2002) proposed a new genus *Spicatella* for a new species *S. bedosae* collected in littoral dunes of southern Vietnam, based on a combination of characters among which its ear-shaped postantennal organ was the most characteristic, but omitted in the species description to compare it to *Delamarephorura*. Another species collected more recently in Madagascar was considered by Thibaud (2008) to be very close to *S. bedosae*. Barra and Weiner (2009) described a second species of *Delamarephorura* from South Africa, *D. szeptyckii*, which is very similar to *D. salti*. The two new species described in this paper, one from South Africa and one from Vietnam, have characters of both *Spicatella* and *Delamarephorura*, making the differences between the two genera indistinct. This led us to carefully re-examine the five concerned species, and propose that *Spicatella* is considered as a synonym of *Delamarephorura*, as shown below. *Delamarephorura* is re-diagnosed accordingly.

Materials and methods

Studied material. – Besides the two new species collected from South Africa and Vietnam, the following specimens were examined for the re-evaluation of the status of *Spicatella* and *Delamarephorura*:

Mesaphorura salti Delamare-Deboutteville, 1953 (type species of *Delamarephorura*): holotype and two paratypes from Tanzania; *Spicatella bedosae* Thibaud, 2002 (type species of *Spicatella*): holotype and 1 paratype from Ca Na (Vietnam); 3 non-type specimens from Binh Chau (Vietnam); *Spicatella* cf. *bedosae*: 5 specimens from Madagascar (Thibaud 2008); *Delamarephorura szeptyckii* Barra & Weiner, 2009: holotype and two paratypes from South Africa (-32.604264°, 26.929138°).

Fresh specimens were cleared in 100 % lactic acid, and permanently mounted on slide in Marc André II. They were observed and illustrated using a Leica DMLB microscope. Specimens were deposited in the South African Museum, Cape Town, South Africa (SAMC), Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland (ISEA), Institute of Tropical Biology, Ho Chi Minh City, Vietnam (ITB) and Muséum national d'Histoire naturelle, Paris, France (MNHN).

Taxonomy

We followed Rusek (1971) and D'Haese (2003) for the annotation of the antennal chaetae, Fjellberg (1991) for tibiotarsal chaetae. The strong reduction of tibiotarsal chaetotaxy and induced shifts in chaeta positions makes uncertain the notation (hence homology) of some dorsal chaetae of tibiotarsi with those of the standard pattern described for Poduromorpha (Deharveng, 1983). The same partly holds for terga chaetotaxy (see Barra & Weiner, 2009: 59).

Abbreviations. – AIIIO, organite of third antennal segment; Abd., abdominal tergum; Ant., antennal segment; PAO, Postantennal Organ; Th., thoracic tergum; Tita, tibiotarsus.

TULLBERGIIDAE Bagnall, 1935

Delamarephorura Weiner & Najt, 1999

Syn.: *Spicatella* Thibaud, 2002: 206

Type species : *Mesaphorura salti* Delamare-Deboutteville, 1953

***Diagnosis.* –** Habitus and dorsal chaetotaxy similar to *Metaphorura* Stach, 1954. Antenna III-organ with two large sensory clubs and two sensory rods protected by three large guard papillae and four guard chaetae dorsally; one large sensory club ventrally. Antennal segment IV with a small simple exsertile vesicle, subapical organite in latero-dorsal position, close to microsensillum; five thickened sensilla. Postantennal organ ear-like with eight to 18 simple, rather large vesicles arranged obliquely to the axis in two regular rows. Pseudocelli faintly double-striate (type II of Weiner & Najt (1991), not type III as hypothesized with doubt by Thibaud (2002)), their formula per half tergite 11/122/22221 or 11/111/11111. Abdomen VI with or without crescentic ridges close to chaeta a2, with two simple anal spines, and often two lateral spiniform processes; chaetae a_0 and p_0 present; a small to minute medioventral process often present. Distal whorl of tibiotarsi I–III with 5 chaetae (ventral chaetae A4 and A5 absent); proximal whorl of tibiotarsi I–III with 3 to 6 chaetae; chaeta M present or absent.

***Discussion.* –** Some chaetotaxic details given in literature descriptions have to be corrected. In the original description of *Spicatella bedosae* (Thibaud 2002: 205, Fig.7) chaeta a_0 on Abd. VI has been overlooked. In the re-description of *Delamarephorura salti* by Weiner & Najt (1999), the tibiotarsal chaeta M is given as absent, while it is actually present. In the description of *D. szeptyckii* Barra & Weiner, 2009, the tibiotarsal chaetotaxy is given as 5,5,4 in row B; it is actually 5, 5, 5, like in most other *Delamarephorura* (Table 1).

The genus *Delamarephorura* keys out near *Dinaphorura* in Dunger and Schlitt (2011) due to the development of spiniform process on Abd. VI (Fig. 1g). However, these processes vary from large to absent in *Delamarephorura* as redefined here, and several other characters of generic value differ between the two genera (especially PAO and AIIIO morphology). Actually, *Delamarephorura* is similar to *Metaphorura* in most characters of supra-generic value, particularly the large size of its three guard papillae of AIIIO (Fig. 1d). The only consistent differences between these two genera is the morphology and arrangement of vesicles in postantennal organ (Fig. 1b, 8 to 18 large, simple vesicles arranged as ear-like *versus* 14 to 28 often bilobed vesicles not arranged as ear-like in *Metaphorura*). However, there are puzzling differences in the published representation of the morphology of both the AIIIO papillae and the PAO vesicles in a species like *M. affinis* (Börner, 1902), suggesting that the discrimination between *Delamarephorura* and *Metaphorura* needs to be re-evaluated, which is beyond the scope of this paper.

Key to known species of the genus *Delamarephorura* Weiner & Najt, 1999

1. Pseudocellar formula: 11/122/22221. Tibiotarsal chaeta M strong…………………………… 2

– Pseudocellar formula: 11/111/11111. Tibiotarsal chaeta M present………………………………………………………………………….***D. capensis* sp. n., South Africa**

2. Strong spine-like processes on abdominal tergum VI present ……………………………………..3

– Spine-like processes on abdominal tergum VI absent or very small……………………………….4

3. Dorsal mesochaetae of relatively large size. Head with chaeta p_2 small, two to three times shorter than p_1. Medioventral process of Abd. VI distinct. Claw with inner tooth….. ………………………………………………………***D. salti* (Delamare-Deboutteville, 1953), Tanzania**

– Dorsal mesochaetae very short. Head with chaeta p2 subequal to p1. Medioventral process of Abd. VI very small. Claw without inner tooth…………………………………………. ……………………………………………………….……***D. szeptyckii*** **Barra & Weiner, 2009, South Africa**

4. Antennal segment IV without a large internal sac distally. Furcal area individualized, devoid of secondary granulation. Tibiotarsal chaeta M absent………………………………….5

– Antennal segment IV with a large internal sac distally. Furcal area not individualized, covered with secondary granulation. Tibiotarsal chaeta M present……………………….. ……………………………………………………………………….***D. bedosae*** **(Thibaud, 2002), Vietnam**

5. Antennal sensilla thick. Tibiotarsal chaeta M absent ……………………………………………………………………...……………………….……***D. tami*** **sp. n., Vietnam**

– Antennal sensilla thinner. Tibiotarsal chaeta M present ……………………………………… ………………………………………………………….….***D.*** **cf.** ***bedosae*** **in Thibaud (2008), Madagascar**

Delamarephorura capensis **sp. n. (**Fig. 1, Table 2)

Material examined. – Holotype: 1 female (deposited in SAMC), South Africa, Western Cape province, Kleinmond, Betty's Bay (-34.35800171, 18.85199928), sandy soil, Berlese extraction, coll. Louis Deharveng & Anne Bedos (SAF-064), 11 March 2008.

Paratypes: 4 paratypes (1 male and 3 juveniles) in SAMC; 4 paratypes (1 male, 1 female and 2 juveniles) in MNHN; 3 paratypes (2 females and 1 juveniles) in ISEA; same data as holotype. Slides were studied under a Leica DM2000 compound microcope with phase contrast and drawings were made using a Leica drawing tube.

***Description.* –** Length. Holotype female: 1.16 mm, paratype male length: 1.07 mm, paratypes juvenile: 0.47-0.55 mm. Colour: white in alcohol. Granulation coarser on dorsal side of the body, with secondary granules larger on axial and lateral areas from Th. I to Abd. IV. Double-striate pseudocelli (type II after Weiner & Najt, 1991), their formula per half terga as 11/111/11111 (Fig. 1A).

Antennal segment IV with five sensilla S1, S4, S7, S8 and S9 (after D'Haese, 2003) = a–e (after Rusek, 1971), a microsensillum, a subapical organite very short, rooting deeply into the integument, and a small exsertile apical vesicle. Antennal III-organ dorsally with two large ovoid sensory clubs and two small sensory rods, protected by three large guard papillae and four guard chaetae; ventrally, one ovoid bent sensory club (Figs. 1C, D). Antennal segment I and II with 7 and 11 chaetae respectively. Postantennal organ ear-shaped, 2.5 times longer than pseudocellus diameter, with 10 (8–12) simple vesicles in two regular rows (Fig. 1B). Labral chaetotaxy: 2/42.

Dorsal chaetotaxy as in Figs. 1A, G and Table 2 with macro-, meso- and microchaetae, sensory chaetae "s" not clearly recognized. Lateral microsensilla on thoracic terga II and III present. Head with chaetae p1 and p2 as microchaetae, p3 as mesochaeta, p4 as tiny microchaeta and p5 as macrochaeta. Abdominal tergum VI with crescentic ridges very faint or absent, dorsal processes absent, a very small ventro-medial process (Fig. 1H) and two anal spines on distinct papillae. Anal spines 1.5 times as long as inner edge of claw and 1.8 times as long as their basal diameter. Thoracic sterna II and III with 1+1 chaetae each.

Ventral abdominal chaetotaxy as in Fig. 1H. Abdominal sternum I with 2+2 chaetae and ventral tube with 4+4 latero-distal chaetae. No fine granulated area on abdominal sternum IV but 2+2 chaetae present in the position of the furcal rudiment.

Tibiotarsi I, II and III with 10, 10 and 10 chaetae (A1, A2, A3, A6, A7 in whorl A; B3, B4, B5, B6 in whorl B; chaeta M present, Figs. 1E, F). Femora I, II and III each with 8 chaetae; trochanters I, II and III with 5, 5, 4 chaetae; coxae I, II and III with 3, 6 and 7 chaetae; subcoxae 2 of legs I without chaetae, of legs II and III, each with 4 chaetae; subcoxae 1 of legs I, II and III with 2, 3 and 3 chaetae. Claw stout, without tooth. Empodial appendage relatively thin and pointed,subequal on all legs, about 1/2.5 as long as inner edge of claw.

Etymology. – The species is named after the biogeographical province where it was collected.

Distribution. – Only known thus far from the type locality, in sandy soil of coastal fynbos vegetation, probably endemic.

Remarks. – *Delamarephorura capensis*, new species, is the only species of the genus with pseudocellar formula as 11/111/11111. See Table1 for other differential characters.

Delamarephorura tami **sp. n.** (Fig. 2, Table 3)

Material examined. – Holotype: 1 female (deposited in MNHN), Vietnam, Kien Giang province, Kien Luong, Hon Chong hills, 10.221674°, 104.613896°, Nui Bai Voi, cirque du Français, soil, Berlese extraction, coll. Quan-Mai (Vn04Hol-055), 2 March 2004. Paratypes: 1 female and 1 male juvenile deposited in MNHN; 1 male juvenile in ITB; 1 male juvenile in ISEA; same data as holotype.

Description. **–** Length. Holotype female: 0.65 mm, paratype male: 0.78 mm. Colour: white in alcohol. Granulation coarser on dorsal side of the body, with secondary granules larger on axial and lateral areas from Th. I to Abd. IV. Double-striate pseudocelli (type II after Weiner & Najt, 1991), their formula per half terga as 11/122/22221 (Fig. 2A).

Antennal segment IV with five rather strong sensilla S1, S4, S7, S8 and S9 (after D'Haese 2003) = a–e (after Rusek, 1971), a microsensillum, a subapical organite very short, rooting deeply into the integument and a small exsertile apical vesicle. Antennal III-organ dorsally with two large ovoid sensory clubs and two small sensory rods protected by three large guard papillae and four guard chaetae, thick; ventrally, one ovoid bent sensory club (Figs. 2C, D). Antennal segment I and II with 7 and 11 chaetae respectively. Postantennal organ ear-shaped, 3 times as long as pseudocellus diameter, with 15 simple vesicles in two regular rows (Fig. 2B). Labral chaetotaxy: 2/42.

Dorsal chaetotaxy as in Figs. 2A, G and Table 3 with macro-, meso- and microchaetae, S-chaetae not clearly recognized. Lateral microsensilla on thoracic terga II and III present. Head with chaetae p1, p2 and p3 as mesochaetae, p4 as microchaeta and p5 as macrochaeta. Abdominal tergum VI with crescentic ridges, two conspicuous dorsal process and two anal spines on distinct papillae; no ventro-medial process. Anal spines 1.3 as long as inner edge of claw and 2.2 times as long as their basal diameter. Thoracic sterna II and III with 1+1 chaetae each.

Ventral abdominal chaetotaxy as in Fig. 2H. Abdominal sternum I with 2+2 chaetae and ventral tube with 4+4 latero-distal chaetae. Fine granulated area on abdominal sternum IV present in the position of the furcal rudiment, with 2+2 chaetae.

Tibiotarsi I, II and III with 11, 11, 10 chaetae: A1, A2, A3, A6 and A7 in whorl A; B1, B2, B3, B4, B5, B6 (B1 absent in tibiotarsus III, Figs. 2E, F); chaeta M absent. Femora I, II and III, each with 9 chaetae; trochanters I, II and III each with 5 chaetae; coxae I, II and III with 3, 6 and 7 chaetae; subcoxae 2 of legs I without chaetae, of legs II and III, each with 4 chaetae; subcoxae 1 of legs I, II and III with 2, 3 and 3 chaetae. Claw without tooth. Empodial appendage relatively thin and pointed, subequal on all legs, about 1/5 as long as inner edge of claw.

Etymology. – The species is named in honor of Truong Quang Tam from ITB of Ho Chi Minh City for his efforts to protect the highly threatened Hon Chong hills where the new species was collected.

Distribution. – Only known thus far from the type locality, in calcareous soil, at about 5 cm depth, under a dense thicket of broadleaved bushes, endemic species.

Remarks. – *Delamarephorura tami* sp. n. is the only species of the genus with 11 chaetae on tibiotarsi I–II and chaeta M absent (See Tab. 1 for other differential characters). The species was collected in calcareous soil, at about 5 cm depth, under a dense thicket of broadleaved bushes. Among the hundreds of soil samples carried out in the Hon Chong hills, *D.* tami, new species, was only found in a single soil core from the “Cirque du Français”, a deep depression that is currently being quarried-out, as will be most of the Bai Voi hill (Fig. 3). *D.* tami, new species, is another endemic species of the Hon Chong karst at risk of extinction, which can be added to the extensive list given by Deharveng et al. (2009).

Scope of contribution of the candidate

Drawings were done by the Dr. W.N. Weiner, photos by Dr. L. Deharveng. Writing and species descriptions were done by the candidate following advice from Dr. L. Deharveng and W.N. Weiner.

References

Bagnall, R. S. (1935) On the Classification of the Onychiuridae (Collembola), with particular reference to the Genus *Tullbergia* Lubbock and its Allies. *Annals and Magazine of Natural History* **10**, 236-242.

Barra, J. A. & Weiner, W.M. (2009) A new species of *Delamarephorura* Weiner & Najt, 1999 (Collembola, Tullbergiidae) from Cape Province (South Africa). *Acta Zoologica Cracoviensia - Series B: Invertebrata* **52**, 57-60.

Börner, C. (1902) Das genus *Tullbergia* Lubbock. *Zoologischer Anzeiger* **26**, 123-131.

D'Haese, C. (2003) Homology and morphology in Poduromorpha (Hexapoda, Collembola). *European Journal of Entomology* **101**, 385–407.

Deharveng, L. (1983) Morphologie évolutive des Collemboles Neanurinae en particulier de la lignée neanurienne. *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse* **4**, 1–63.

Deharveng, L., A. Bedos, Le Cong Kiet, Le Cong Man & Truong Quang Tam (2009) Endemic arthropods of the Hon Chong hills (Kien Giang), an unrivaled biodiversity heritage in Southeast Asia. In: Le Cong Kiet, Truong Quang Tam & Ly Ngoc Sam (eds.), *Beleaguered Hills: Managing the biodiversity of the remaining karst hills of Kien Giang, Vietnam*, Nha Xuat Ban Nong Nghiep, TP. Ho Chi Minh. Pp. 31-57.

Delamare Deboutteville, C. (1953) Collemboles du Kilimanjaro récoltés par le Dr. George Salt. *Annals and Magazine of Natural History* **12**, 817-831.

Dunger, W. & Schlitt, B. (2011) Tullbergiidae. In: Dunger, W. (ed.), *Synopses on Palaearctic Collembola*. Volume 6/1. Senckenberg, Museum of Natural History Görlitz. 168 pp.

Fjellberg, A. (1991) Tibiotarsal chaetotaxy in Tullbergiinae. *Entomologica Scandinavica* **21**, 431-434.

Rusek, J. (1971) Zur Taxonomie der *Tullbergia* (*Mesaphorura*) *krausbaueri* (Börner) und ihre Verwandten (Collembola). *Acta entomologica bohemoslovaca* **68**, 188–206.

Stach, J. (1954) *The Apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: Onychiuridae*. PWN, Kraków, 219 pp.

Thibaud, J.-M. (2002) Contribution à la connaissance des collemboles interstitiels des sables littoraux du Vietnam. *Revue française d'Entomologie* (N.S.) **24**. 201–209.

Thibaud, J.-M. (2008) Les collemboles des sables littoraux de Madagascar. *Annales de la Société entomologique de France* **44**, 503–513.

Weiner, W. M. & Najt, J. (1991) Collemboles Poduromorpha de Nouvelle Calédonie. 6. Onychiuridae Tullbergiinae. In: J. Chazeau, S. Tillier (eds). Zoologia Neocaledonica, 2. *Mémoires du Muséum national d'Histoire naturelle A* **149**, 119-130.

Weiner, W. M. & Najt, J. (1999) New genus of Tullbergiinae (Collembola). *Annales de la Société Entomologique de France (N.S.)* **35**, 183-187.

Tables

Table 1 - Differential characters of the species of *Delamarephorura.*

	D. salti	*D. szeptyckii*	*D. bedosae*	*D.* capensis	*D.* sp. n 2	*D.* cf *bedosae*
Size	1.5	0.77-0.86	0.40-0.55	1.07-1.16	0.65-0.78	up to 0.7
Pseudocellar formula	11/122/22221	11/122/22221	11/122/22221	11/111/11111	11/122/22221	11/122/22221
Large internal sac apically on ant. IV	absent	absent	Present	absent	absent	absent
PAO: number of vesicles	14 or 15	12	12 to 18	8 to 12	15	15 or 16
Number of chaetae of tibiotarsi	10, 10, 9	10, 10, 10	10, 10, 10	10, 10, 10	11, 11, 10	10, 10, 10
Tita: chaeta M	present	present	Present	present	absent	present
Tita: whorl B*	B3B4B5(B6)	B3B4B5B6	B3B4B5B6	B3B4B5B6	(B1)B2B3B4B5B6	B3B4B5B6
Secondary granules on furcal area	absent	absent	Present	present	absent	absent
Crescentic ridges	present	well marked	Indistinct	absent or very faint	present	indistinct
Dorsal spine-like processes	present	present	Absent	absent	present	very small
Ventro-medial process	present	very small	very small	small	absent	small
Distribution	Tanzania	South Africa	Southern Vietnam	South Africa	Southern Vietnam	Madagascar
Ecology	about 4000 m a.s.l.	grassland, 1600 m a.s.l.	seashore	sandy soil under bushes, sea level	lowland secundary forest, in soil	seashore

* between brackets, chaetae absent on Tita III

Table 2. Formula of dorsal chaetotaxy per half tergum (scx, subcoxa 1; pl, abdominal pleurite) of *Delamarephorura* capensis.

Terga / Chaetae rows	Th.I	Th.II	Th.III	Abd.I	Abd.II	Abd.III	Abd.IV	Abd.V
A	–	5^1	5^1	5^4	5^4	5^4	5^7	5^8
M	–	4^2	4^2	1^5	1^5	1^5	–	–
P	4	4^3	4^3	5^6	5^6	5^6	5^9	3^{10}
scx/pl	2	3	3	2	3	3	6	2

1 – a4 absent; 2 – m1, m4, m5, m6=s present; 3 – p2, p6 absent; 4 – a6 absent, 5 – m5 present; 6 – p5 absent; 7 –a3 absent; 8 – a6 absent, 9 – p3 absent, 10 – p2, p4, p5 present.

Table 3. Formula of dorsal chaetotaxy per half tergum of *Delamarephorura* tami.

Terga / Chaetae rows	Th.I	Th.II	Th.III	Abd.I	Abd.II	Abd.III	Abd.IV	Abd.V
a	–	5^1	5^1	5^4	5^4	5^4	5^7	5^8
m	–	5^2	4^2	1^5	1^5	1^5	–	–
p	4	4^3	4^3	5^6	5^6	5^6	5^9	3^{10}
scx/pl	2	3	3	2	3	3	6	2

1 – a4 absent; 2 – m1, m3, m4, m5, m6=s present; 3 – p2, p6 absent; 4 – a4 absent, 5 – m5 present; 6 – p5 absent; 7 –a3 absent; 8 – a3 absent, 9 – p3 absent, 10 – p2, p5, p6 present.

Figures

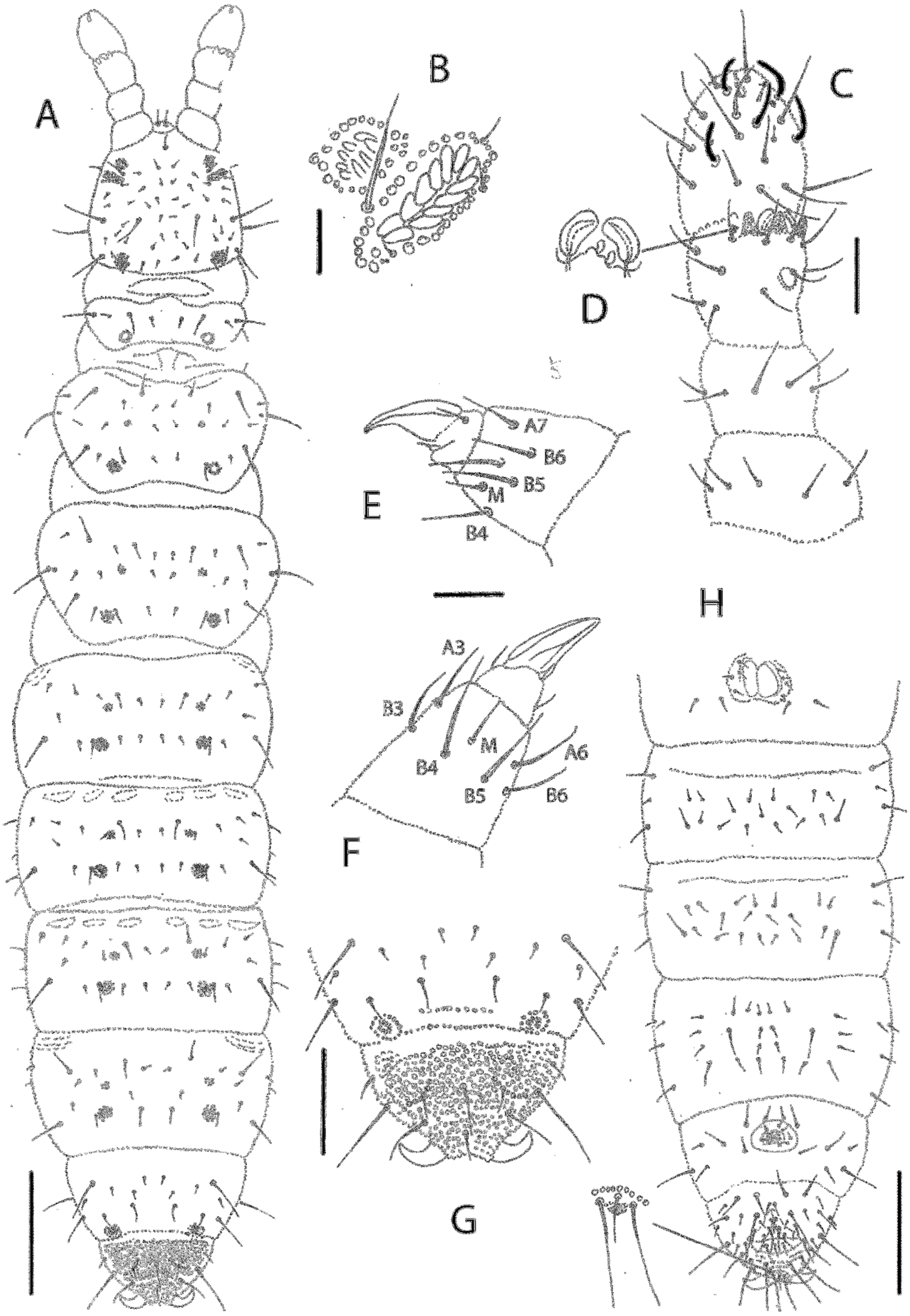


Fig. 1. *Delamarephorura sp. 1*, new species: A–dorsal chaetotaxy; B–postantennal organ and pseudocellus; C–antenna; D–antenna III-organ: sensory clubs and sensory rods; E–ventro-lateral view of tibiotarsus III; F–ventral view of tibiotarsus III, other specimen; G–chaetotaxy of abdominal terga V and VI; H–ventral chaetotaxy of abdomen, with ventral process of abdomen VI. Scale bars: 0.1 mm (A, H), 0.05 mm (G), 0.01 mm (B, C, E and F). Drawings: W.M. Weiner.

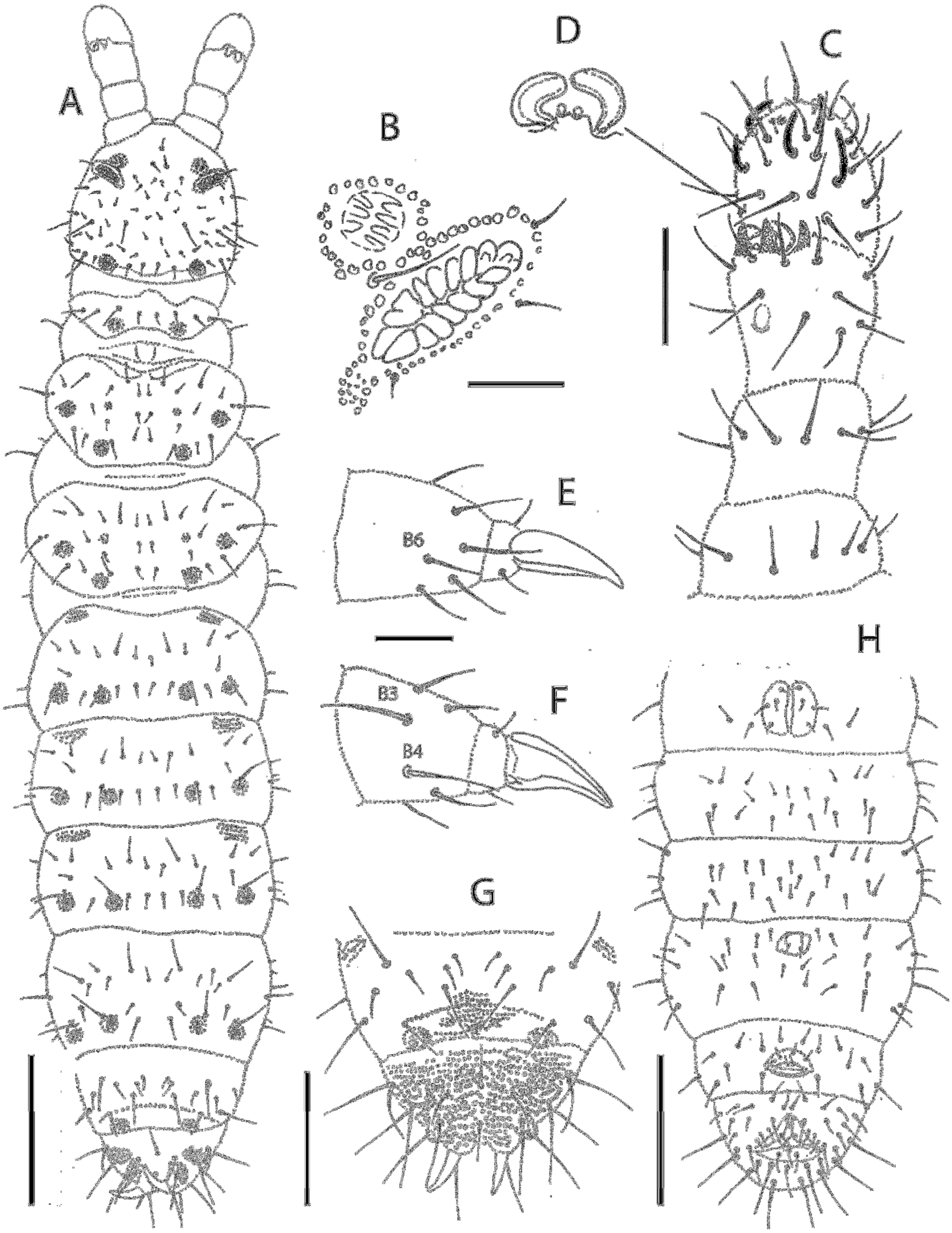


Fig. 2. *Delamarephorura sp. 2*, new species: A–dorsal chaetotaxy; B–postantennal organ and pseudocellus; C–antenna; D–antenna III-organ: sensory clubs and sensory rods; E, F–tibiotarsus III; G–chaetotaxy of abdominal terga V and VI; H–ventral chaetotaxy of abdomen. Scale bars: 0.1 mm (A, H), 0.05 mm (G), 0.01 mm (B, C, E and F). Drawings: W.M. Weiner.

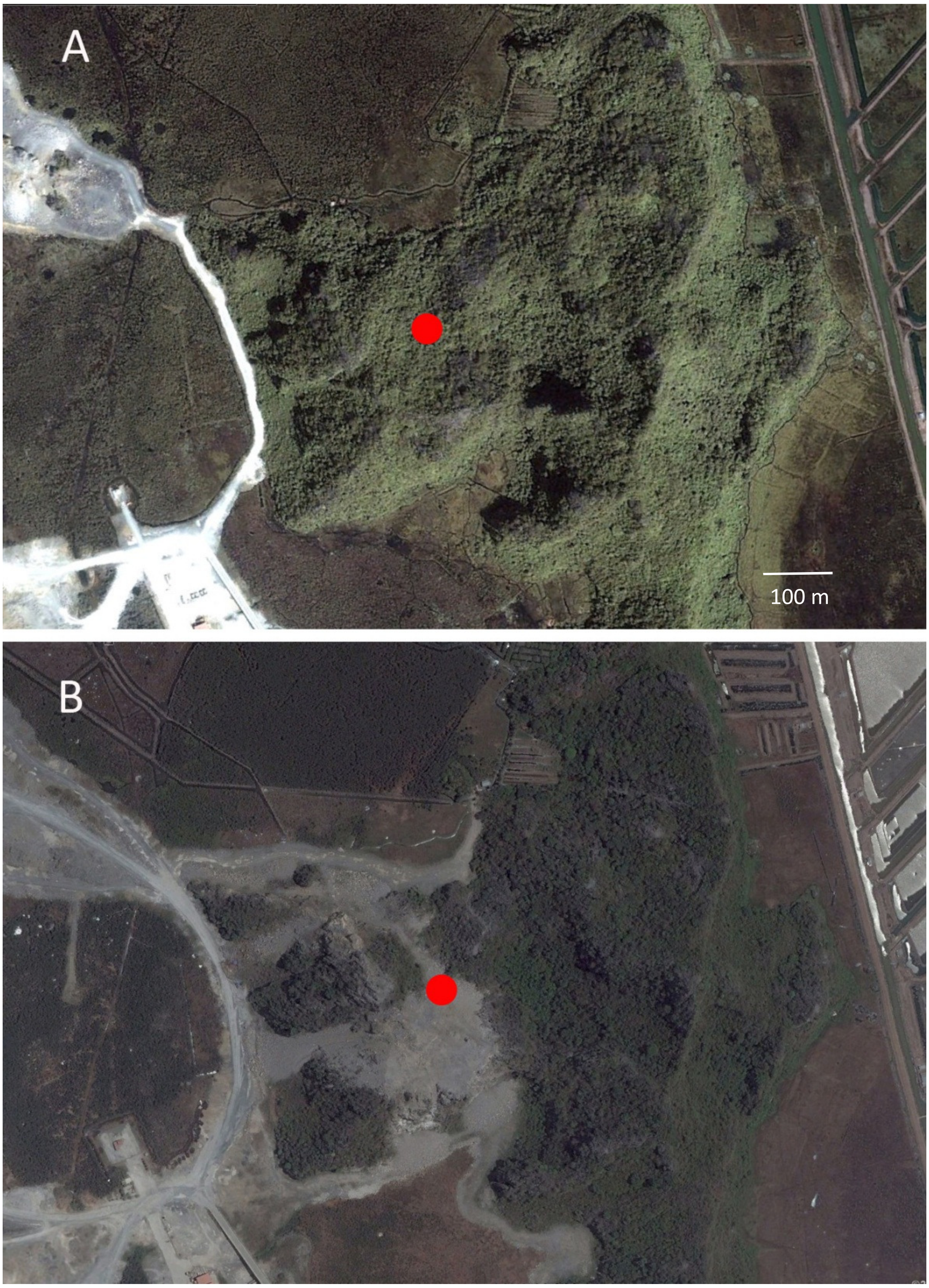
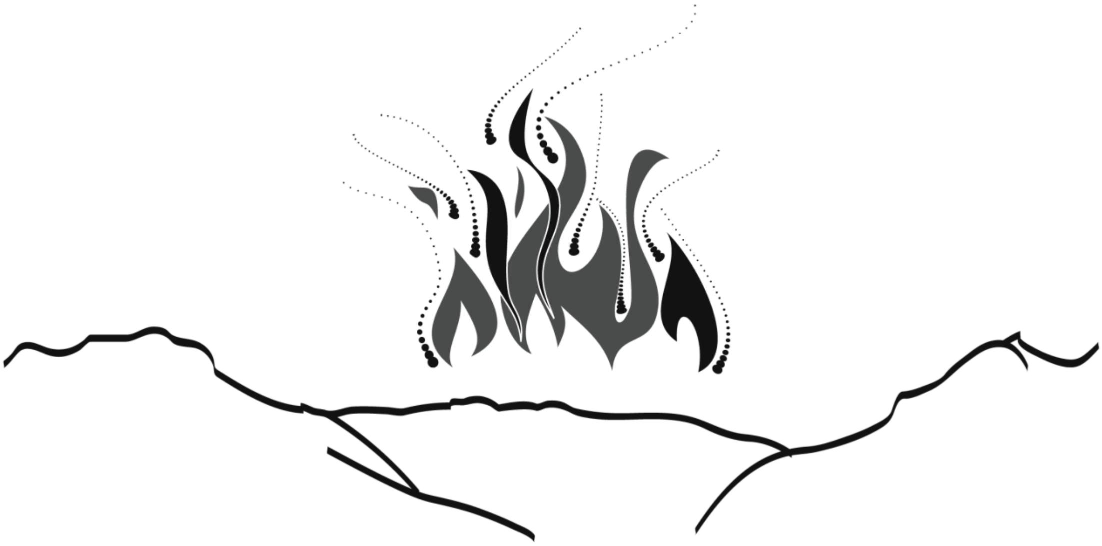


Fig. 3: Satellite view of Bai Voi hill (Kien Giang province, Vietnam, 10.221674°, 104.613896°) in 2006 (A) and in 2011 (B), illustrating the destruction of the type and only known locality (indicated with a red dot) of *Delamarephorura tami*, by limestone quarrying (dates of the photos were inverted in Google Earth consulted in December 2011).

Chapter 6

The resilience of fauna in a fire-prone vegetation type:

Springtails as exemplars



Introduction

The rate and extent of anthropogenic environmental change are on the increase. The numbers of extreme high temperature events are growing (Hansen et al. 2012), glacial melt rate is increasing (Rignot et al. 2011), and biological invasions are becoming more common (DAISIE 2009). Habitat disturbance is likewise continuing globally, with major impacts both inside and outside protected areas (MEA 2005; Laurance et al. 2012). In many ecosystems, fire is a major natural form of disturbance (Syphard et al. 2009). Although long used by humans to alter landscapes (Bond & van Wilgen 1996, Bond & Keeley 2005, Bond et al. 2005), in many areas fire regimes have substantially been altered over the last several decades (Goldammer & Price 1998, Syphard et al. 2009). Often these changes have been associated with specific conservation management goals, and fire is widely used as a tool for biodiversity management in protected areas (Sutherland & Dickman 1999, Smucker et al. 2005, Pastro et al. 2011, van Wilgen et al. 2011, Fontaine et al. 2012, Kelly et al. 2012). However, evidence is growing that fire regimes are also shifting as a consequence of changing climates and growing human populations (Stocks et al. 1998, Goldammer & Price 1998). The fire-prone fynbos vegetation of the Western Cape of South Africa provides a clear example. Depending on annual rainfall, fire return times in the absence of human intervention should be in the order of seven to 29 years (van Wilgen & Hensbergen 1992, van Wilgen 2009). However, it now appears that, whether or not management attempts are made to alter the fire cycle, return times are declining substantially (van Wilgen 2009, van Wilgen et al. 2011). Key drivers of the change appear to be growing human populations and warming climates (Pierce et al. 2004, Syphard et al. 2009).

Despite the significance placed on fire worldwide, current understanding of the effects of fire on soil invertebrates is relatively poor. In South Africa, the known effects of fire on animal species richness and density have come largely from research on vertebrate groups such as mammals and birds (e.g. Dean 1987, Bond 1997). By comparison, studies on invertebrates remain few and fragmented. Studies on invertebrates have been undertaken mainly in the grassland and savanna biomes on grasshoppers (Chambers & Samways 1998), ants (Fraser 1990, Parr et al. 2002, Parr et al. 2004), Coleoptera (Gandar 1982), termites (Ferrar 1982) and mites (Hugo-Coetzee & Avenant 2011). Acknowledging the difficulty of obtaining natural pre- and post-fire diversity data, several of these studies vary in design, scale and replication making generalisations difficult, also compounded by poor reporting of the sample unit size, area investigated and extent of fire (see Parr & Chown 2003). Surprisingly, very few of these studies have been done in the small, fire-prone Fynbos Biome. Studies here have mainly focused on ants (Donnelly & Giliomee 1985, de Kock et al. 1992), but more recently Pryke & Samways (2012) used multiple groups of invertebrates (but at the higher, not species, taxonomic levels), showing that morpho-species richness and assemblage composition of most groups recovered within three years after the fire.

Understanding how biodiversity is responding and will continue to respond to changing disturbance regimes is a key prerequisite for evidence-based conservation (Hobbs & Heuneke 1992). Such information is essential for arguments in favour of mitigation, and for developing strategies to adapt to change given evidence of on-going increases in its rate and scope. Developing understanding across a full range of taxa is especially important for reducing uncertainty about how responses might vary among different functional groups that are significant in sustaining ecosystem functioning (Decaëns et al. 2006). In the case of a disturbance such as a fire, much work has been done on the responses of vegetation and significant taxa such as birds and mammals, with increasingly sophisticated understanding of interactions among them and how global change may impact these interactions (Dean 1987, Bond 1997, Bond et al. 2005, Root et al. 2003, Pastro et al. 2011). For some invertebrate groups similar sophisticated understanding is being developed. For example, ant abundance significantly increases after fire, thus they seem to be highly resistant and resilient to fire (Parr et al. 2004, Parr & Andersen 2008, Lach et al. 2009, Vasconcelos et al. 2009). Much of this work benefits from investigations across a range of ecosystems globally, contributing to growing understanding of the resilience of assemblages to changing fire regimes and a reduction in uncertainty concerning the likely outcomes of management interventions (van Wilgen et al. 2011). By contrast, for other invertebrate groups, investigations are much more limited, making generalizations problematic despite the functional significance of these groups (Parr & Chown 2003). This is true particularly of the springtails, an important group of soil organisms.

Soil organisms play a major role in soil ecosystem functioning (Wardle et al. 2004). One such group is springtails, which have been suggested to play an important role in litter decomposition and the formation of soil microstructure (Rusek 1998, Hopkin 1997). Although their role in soil ecosystems is widely appreciated, how they respond to fire has not been extensively investigated. Current generalities, that springtail abundance initially decreases significantly after fire and gradually increases again, have mostly been derived from investigations from temperate forests in Europe and North America (Malmström et al. 2009, Huebner et al. 2012, Malmström 2012). On the other hand, it appears that springtails are highly resilient to fire (Renschin et al. 2004). How assemblages elsewhere respond to change is not as well understood (but see Greenslade & Smith 2010), even though fire prone ecosystems globally have rich springtail faunas.

The resilience of populations or ecosystems has been increasingly studied since the initial introduction of the term by Holling (1973). It has been defined as the rate as which population density returns to equilibrium after a disturbance (Pimm 1991). Several factors affect the resilience of a population operating at different spatial and temporal scales. These include life history traits, functional diversity, or how quickly nutrients are available after a disturbance event (Pimm 1991), with increased functional diversity increasing the resilience of a population (Peterson et al. 1998, Elmqvist et al. 2003). Due to rapid environmental change and consequently the increased need to manage natural ecosystems (MEA 2005), understanding resilience is important to predict how species will respond to disturbance (Peterson et al. 1998). After a disturbance event (such as a fire), the colonization of new surfaces during primary succession can be measured as a change in species richness and abundance over time. During these events, plant species may influence the quality and amount of resources available to the belowground organisms (Wardle 2002). Typically, plant species that produce poor quality resources tend to support lower abundances of soil fauna than higher quality producing plant species (Wardle 2002).

Given this situation here I examine the effects of a large-scale fire on the springtail fauna of a fynbos ecosystem in the Western Cape of South Africa. Fire regimes are changing substantially in this vegetation type by increasing in frequency (van Wilgen 2009). Moreover, recent work has highlighted the fact that nutrient turnover through decomposition is driven not only by fire in this system, but also by biotic decomposition (Bengtsson et al. 2011, 2012). Elsewhere variation in decomposition rates has been shown to have significant impacts on springtail faunas, and changing litter availability is likely to affect the faunas (Pflug & Wolters 2001). Moreover, understanding of the resistance and resilience of soil faunas to fire in the region is not well developed. To date work has been done on ants (de

Kock et al. 1992, Vorster 2011) and various arthropod groups (Pryke & Samways 2012). For springtails the investigations are typically restricted to the group as a whole, with little understanding of variation in diversity. Although understanding of wholesale changes in taxonomic groups is important, understanding of the effects on ecosystem functioning must necessarily be concerned with investigations at the species and functional group levels. However, it is not clear if they show the same patterns. Therefore, in this study I focus on changes in the variation in species composition and functional diversity of springtails across a four year period characterized by a major fire event at the end of the first year of sampling. In particular the following questions are asked:

i. What is the variation in abundance and diversity of springtails with different types and quality of litter?
ii. What is the impact of a fire event on the springtail assemblages? Here, I characterize the impacts of fire, investigating both the resistance of the assemblage (i.e. change after one year) and its resilience (return to a pre-fire state). Although this four year period is slightly less than the return time for fynbos in such high rainfall regions (c. 4-7 years) (Forsyth & van Wilgen 2010), fire frequency has also increased substantially over the last few decades due to an increase in human population and accidental ignition.

Methods

Study sites and experimental technique

The study was carried out during the winter months (mid-March – mid-September) in Jonkershoek Nature Reserve, South Africa (S33°59.341, E018°57.458), which is approximately 9 km from Stellenbosch and encompasses 14 527 hectares (van Wilgen & McDonald 1992). The area has a Mediterranean climate with warm, dry summers and cool, wet winters. The summer months, which coincide with high winds and high radiation, are typically periods of extreme fire hazard (Versfeld et al. 1992). The mean temperature was found to be 16.2°C (lowest minimum 0.2 °C and highest maximum 39°C) and the annual rainfall 1523 mm (Versfeld et al. 1992). The vegetation consists of mainly mountain fynbos (Rebelo et al. 2006).

To assess the diversity and distribution of springtails, the litterbag method was used for sampling (Bocock & Gilbert 1957). Litterbags are a standard and appropriate method to sample soil fauna, and have proven to be extremely efficient during a previous study on decomposition rates (Bengtsson et al. 2011, 2012). By using a standard amount of litter, the litterbag method not only provides an estimate of the springtail diversity, but also the decomposition rate of the litter. In addition, whilst pitfall traps may give an indication of the surface dwelling species, litterbags can also be used to collect soil species. The litterbags consist of individually numbered cylindrical plastic containers with a height of 4 cm and a diameter of 7.5 cm and a removable lid with steel mesh size (1.6 mm) to allow animals to enter the litterbags, while the bottom consists of a steel mesh with a size of 0.5 mm (see Supplementary material Figs. 1A, B).

Litterbags containing three different types of litter were used. It has been shown that springtails differ in abundance and richness between different litter types (Liu et al. 2012, and H.P. Leinaas et al. unpublished results). Thus to capture the overall diversity of springtails, three different litter types were used (see Bengtsson et al. 2011, 2012). The plant species used represent the major plant species which are characteristic of the fynbos (see Rebelo et al. 2006). These consisted of litter from the plant species *Erica multumbellifera*, *Restio multiflorus* and a hybrid *Protea exima* x *Protea susannae*, var. “silva” and “cardinal”. The *Erica* litter were collected at Heuningbos, Kleinmond (-34.330600°, 19.060950°), the hybrid from Flower Valley, Gansbaai, the *Protea* litter from Flower Valley Farm, Stanford (-34.548923°, 19.470345°). This is referred to as the *Erica-Protea* mixture. Second, Restio litter was collected at White Water Lodge, Stanford (-34.4048996, 19.53969955). A third litter type was included, namely *Galenia africana* (Aizoaceae), a common shrub in the Western Cape up to 1.5 m tall. It is an indicator of disturbance such as overgrazing and its decomposition rate has been well recorded (Allsopp 1999). This species was collected from an overgrazed rangeland west of the Paarl Mountain (-33.727436°, 18.893114°), where it is the dominant shrub in the vegetation. *Galenia africana* was used as a standard litter to be compared between sites, and to include a nutrient rich litter as has been done previously (Bengtsson et al. 2011).

Litter was prepared by collecting plant material of the chosen plant species in the field where they occur in high numbers, at the end of the dry season, by cutting the outer 10-20 cm of branches of live plants. The material were taken to the laboratory, dried at 40° C for at least 24 hours and then stored in open containers at room temperature. The dried plant material was cut into approximately 1 cm long pieces. In the laboratory, the litterbags were filled with air-dried litter up to approx. 3.5 cm and be weighed to nearest 0.1 mg on an electronic balance (FA304T, Avery Berkel, Fairmont, USA). The litter was not compressed but allowed to maintain its normal volume and density. The filled litterbags were stored dry at room temperature before being deployed in the field. The mean amounts of litter used were: *Galenia* 9.8 ± 0.6 g, *Restio* 8.5 ± 0.3 g, and *Erica-Protea* mixture 11.2 ± 0.8 g. The data on litter mass was used to calculate the decomposition rates of the litter types. These results have been used in publications where the candidate was involved with in a previous study (Bengtsson et al. 2011) involving litterbags, and the current study (Bengtsson et al. 2012, see Appendix 3, 5).

Two study sites were selected, one Proteoid and one Ericoid, which were 200 metres apart. These study sites were chosen to represent the major plant species characteristic of Fynbos, which include *Protea*, *Erica* and *Restio* (Rebeleo et al. 2006). A Restioid site was initially included, but was excluded in years after the fire due to flooding. The Proteoid site was dominated by *Protea nitida*, while the Ericoid site was dominated by *Erica hirta* (see Supplementary material Figs. 3A, B). Three litterbags each containing a different litter type (*Protea-Erica* mixture, *Restio* and *Galenia*) litterbags were deployed under the dominant plant species in the respective sites at the end of summer (March/April), left undisturbed and subsequently collected in September (2008) or in July or August (2009-2011). Litterbags were deployed in an L-shape transect (estimated sample unit coverage of 2500 m^2) to cover a wider area of each of the proteoid and ericoid sites (10 litterbags of each litter type per site, resulting in a total of 60 litterbags, Supplementary material Fig. 11). Each tree or shrub underneath which litterbags were deployed was approximately 10 metres apart. The litterbags were deployed under the trees or shrubs within 3-4 cm from another, less than 40 cm from the bush base, on the south-west to south-east side to minimise sun exposure. They were placed in the soil with the top of the litterbags at ground level which allows invertebrates to enter from the top. In 2008 the litterbags were placed in the field on 10 March 2008 and collected on 8 (litterbags 1-5) or 17 (litterbags 6-10) September 2008 (separate dates due to extraction capacity reasons).

During February 2009 an unplanned fire swept through the Jonkershoek Nature Reserve and burnt the majority of the reserve, including the entire areas of the proteoid and ericoid sites used in 2008 (Supplementary material, Fig. 2). The fire in this study was a single wildfire, thus replication was not possible. Previous fires in this area burned in 1927, 1942, 1958 when the whole area burnt, in 1936 and 1973 when the area partially burnt, and finally in 1977 and 1987 when prescribed burning was done (van Wilgen & McDonald 1992). After the fire in 2009, litterbags were deployed on 15 April 2009, 4 May 2010 and 27 May 2011, and collected on 30 July 2009, 12 August 2010 and 5 September 2011 (Supplementary material, Figs 3-7). The shorter period in the field (three months) was chosen for the following reasons: Firstly, there is little decomposition and hence biological activity before the onset of winter rains in April and May. Secondly, I sampled the litterbags earlier than in 2008, because I wanted to avoid the risk of extended periods of drought at the end of the winter influencing the results. The litterbag method to collect springtails may be less efficient if the sampling is preceded by longer dry periods (H.P. Leinaas et al., unpublished results). Finally, by 2009 the decomposition rate was known for *Galenia africana* (half-life = 100 days; Bengtsson et al. 2011, 2012), and hence approximately 3 months was chosen from 2009 onwards. The overall consequence of this change in method is that the results for 2008 are likely to be conservative, as the sampling may have been less efficient than later years. However, in 2008 late August and early September had >200 mm rain and a mean temperature of 11.1 °C (Cape Nature data, unpublished) in the month preceding sampling, which means that springtail abundances in the litterbags most probably was little affected by droughts.

Upon collection of the litterbags, they were wrapped in aluminium foil to prevent any animals from escaping and immediately placed individually in plastic bags and stored upright in a cool, thermally insulated container and returned to the laboratory within two hours of collection. The litterbags were transported to the laboratory at Stellenbosch University, and extracted using a modified high-gradient extractor (Central Mechanical Services, Stellenbosch Engineering, Stellenbosch University, Supplementary material, Fig. 8). If litterbags could not be extracted immediately (due to the capacity of the high gradient extractor), they were stored at 10° C until extraction could be done, but not for longer than two hours. Litterbags were inverted in the high gradient extractor with heating from above (see Macfadyen 1953, Block 1966) and cooling from below by means of a temperature controlled water bath (Grant R2, Cambridge, UK). The high gradient extractor temperature was at about 25 °C when the litterbags were inserted, and gradually increased to 50 °C over a period of four days. The extraction was done into 100% propylene glycol (using ethanol would deter animals from descending through the litter and the possibility of molecular analyses is still adequate, van Vuuren pers comm.). The extraction took approximately four days. Hereafter, the animals were transferred to 99.9% ethanol for identification. The dry litter samples in each litterbag were transferred to aluminium foil and dried at 50 °C for at least 24 hours to ensure that the samples are dry before storage. Little organic material was lost during the extraction process.

Morphospecies were identified using taxonomically significant morphological characters and European keys available to determine the family or possibly the genus level (Fjellberg 1998, 2007, Bretfield 1999, Potapov 2001, Hopkin 2007). Amongst others, the characteristics used included the arrangement of chateta on the body (chaetotaxy). In addition, taxonomists were consulted on a regular basis as part of an existing knowledge transfer project (see Janion et al. 2011b).

Statistical analyses

Data from two samples were removed prior to analyses, as these contained over 5000 individuals of *Cryptopygus* sp. each, which were mostly juveniles. There is a possibility of animals breeding in the litterbag, which may result in an artificial high abundance. Thus, compared to the abundance (i.e. mean number of Collembola per litterbag) values for other samples, I elected not to include data from these two samples to remove any bias caused by breeding in the litterbag.

Collembola were divided into the major orders, Symphypleona, Entomobryomorpha and Poduromorpha (only one individual of Neelipleona was found so were excluded in the following analysis), as springtail orders provide a first proxy for functional group differences (Hopkin 1997). The mean abundance and species richness were compared within each major order between years, using a generalized linear model with a quasi-Poisson distribution, as it has been shown that different functional groups respond differently to disturbances such as fire (Malmström 2012). For example, species in the group Symphypleona are usually plant feeders and are known to mostly occur on the vegetation, while species in the group Poduromorpha are mostly fungi or algae feeders and thus litter or soil dwellers (Hopkin 1997).

Sampled-based rarefaction curves were plotted to examine the degree of sampling efficiency and to determine the predicted number of species in each site in each year, using Chao1 and Jacknife 2 in EstimateS V8.2.0 (Colwell 2009). Jacknife 2 does not require data to be normally distributed and provides conservative but accurate estimates (Magurran 2004). Sampling is considered adequate when the rarefaction curves and the estimators converge at the highest observed values (Longino et al. 2002). Jacknife 2 estimates were calculated for each year of sampling. Two different estimates were calculated, first without replacement which is more accurate (Colwell 2009), and second with replacement following 500 randomisations. The latter enables one to calculate a variance estimate. Rank-abundance curves were plotted to visually display the species' abundances per year.

A Generalized Linear Model with a Quasi-poisson distribution was used to calculate the effect of fire, litter type and site on the species richness and abundance of species. Each site was analysed separately, as site had a significant effect on species richness and abundance (Table 4A). A quasi-Poisson model was used as the data were overdispersed, and all analyses were done without log transformation, as recent studies showed that count data performed better when data is not transformed (O'Hara & Kotze 2010). If any interactions between variables were found not to be significant, the interaction term was removed (after Crawley 2007). All analyses were undertaken in R version 2.15.1.

To investigate the resilience (as turnover) of the assemblages between years and sites, beta diversity was calculated between sites and years using a method recently proposed by Carvalho et al. (2012), which distinguishes between the contribution of species replacement and species richness. To do this I used a presence-absence matrix of the species per site and year. First, I calculated the B_{cc} complementary measure (Colwell & Coddington 1994), also known as the Jaccard dissimilarity measure:

$$Bcc = \frac{b+c}{a+b+c}$$

where *a* is the number of species common to both sites (in this case years), *b* is the number of species exclusive to the first site, and *c* is the number of species exclusive to the second site.

Replacement (B_{-3}) is calculated as the substitution of *n* species in one site from *n* species in another site (Carvalho et al. 2012).

$$B_{-3} = \frac{2 \times \min(b, c)}{a + b + c}$$

B_{rich} is the absolute difference in species richness between sites is calculated by:

$$B_{rich} = \frac{|b - c|}{a + b + c}$$

Thus, according to Carvalho et al. (2012) beta diversity (B_{cc}) consists of two components, replacement (B_{-3}) and species richness (B_{rich}) differences:

$$B_{cc} = B_{-3} + B_{rich}$$

The values obtained for each measurement were assigned to a dissimilarity matrix and analysed using a cluster analysis in Primer V.6.0 (no transformation of data), resulting in a dendrogram to illustrate the change in assemblages through time.

To assess the change in community assemblage composition between years, multivariate community analyses were undertaken in Primer V.6.0 (Clarke & Warwick 2001). Data were square root transformed to reduce the weight of the common species (Clarke & Warwick 2001), and a Bray-Curtis similarity index was used to calculate similarities in species composition. Non-parametric analyses of similarity (ANOSIM) were used to establish if there were differences in springtail assemblages before and after the fire. Global R values obtained from ANOSIM were used to determine the degree of similarity between years, thus the closer R is to 1 the more dissimilar the species assemblages are, while an R-value close to zero indicates that the assemblages are not separable. A non-metric multi-dimensional scaling (nMDS) ordination was used to plot the differences between years. This analysis was repeated using only presence-absence data, to distinguish the effect of the abundant species.

To assess the contribution of specific species between years and sites, SIMPER was undertaken in Primer V.6.0 (Clarke & Warwick 2001). This analysis mainly identifies the species providing the discrimination between two observed assemblages (Clarke & Warwick 2001). Data was square root transformed to reduce the weight of common species, and a Bray-Curtis similarity index was used, with *Year* and *Site* as factors. The cut-off was set at 90% (Clarke & Warwick 2001). This analysis was repeated using presence-absence data.

Results

A total of 53,379 springtails, comprising 35 species in 31 genera and 14 families were found (Table 1, 3). The sample based rarefaction curves reached an asymptote in most cases (Figs. 1A-D, Table 1). Species richness and abundance differed significantly between sites (Table 4A). The highest total species richness and total abundance was observed three years after the fire (2011) (Table 1, 3, Supplementary material, Fig. 10). Mean species richness was highest in the *Protea* site two years after the fire (7.67 ± 0.36), while mean abundance was highest in the *Erica* site three years after the fire (702.43 ± 317.9, Table 2, Figs. 2, 3). One and two years after the fire species richness was significantly different, while there was a significant interaction in the *Protea* site one and three years after the fire (Table 4A). Species richness did not differ consistently among sites (no main effect but a site x year interaction) whereas abundance did (Table 4A). All the litter types had a significant effect on Collembola abundance, while year (2010 and 2011) also had a significant effect (Table 4A). However, when the sites (*Erica* and *Protea*) are analysed separately, species richness is only affected by year in the both sites and no interactions were found.

For all the orders investigated, year (i.e. fire event) had a significant effect on species richness, while litter, site and year had a significant effect on the abundance (Table 5). The order Poduromorpha showed a slight decrease in mean abundance after the fire, which slowly increased after the fire (Fig. 4C, Table 5A). For this group there was also a rapid increase in abundance three years after the fire in the *Protea* site. The order Symphypleona showed a decrease in abundance one year after the fire, increased again two years after the fire and slowly decreased again (Fig. 4A, Table 5C). Year had a significant effect on species richness for the Symphypleona, while litter types and year had an effect on abundance. Similarly, for the order Entomobryomorpha, (Fig. 4B), *Galenia* litter had a significant effect on abundance, and a *Galenia* litter x year interaction was also found to be significant (Table 5B).

Species richness was significantly influenced by year in both the *Protea* and *Erica* sites, but not by litter (Table 4B, Fig. 5A, C). The interaction between litter and year was not significant (F = 0.52, p=0.79). Springtail abundance was significantly influenced by litter and year in the *Erica* site, while the interaction between litter and year was not significant (F=1.81, p=0.1039). In the *Protea* site, no effect of litter and year alone, but the litter and year interaction significantly influenced springtail abundance (Table 4B). The interpretation of this interaction is complicated, but it's likely that the litter quality may be driving these interactions (also see Bengtsson et al. 2012).

Results from the Analysis of Similarity (ANOSIM) when using square root transformed abundance data, had a higher R value (Global R=0.135, p=0.286, Fig. 6A) than when using presence-absence data only (Global R=0.047, p=0.457, Fig. 6B), although neither were significant. A *Global R* value closer to 1 indicates more dissimilarity. Thus, the relative abundances of the species may be more important here than species richness or identity.

The beta diversity analyses indicate that turnover is higher between years than between sites (B_{cc}), especially the first years after the fire (Fig. 7A). The dendrogram for B_{-3} clearly indicates that species replacement (Fig. 7B) is more important in the recovery of the assemblages than species richness differences ($B_{rich,}$ Fig. 7C).

Figure 8 shows a presence-absence matrix of the species before and after the fire. It illustrates very clearly how certain species such as *Brachystomella* sp., *Isotomurus* sp. and *Paristoma* sp. are present in the sites before and after the fire, while others are either present or absent directly after the fire or after a few years.

From the SIMPER analysis, the top three species discriminating between assemblages between years were *Cryptopygus* sp., *Triacanthella* sp. and *Parisotoma* sp. (Supplementary material Table 1). Average dissimilarity was high between all years (63.44 % - 73.39 %) as well as between sites (70.2 %). When the SIMPER analysis was repeated using presence-absence data, other species were found to be discriminating between assemblages, such as

Brachystomella sp., *Lepidocyrtus* sp. and *Seira* sp. 1 (Supplementary material Table 2). However, when comparing the *Erica* and *Protea* sites, *Triacanthella* sp. and *Cryptopygus* sp. was still contributing more than others.

Discussion

In this study, epigaeic springtail species (surface-dwelling species), especially the Symphypleona, showed a significant decrease in species richness and abundance after the fire. Similar results have also been found in studies of forest springtails (Malmström et al. 2009, Greenslade & Smith 2010). Despite the severe effect of fire on springtail abundance in this study, their recovery was remarkably quick. In less than three years, all groups of springtails had recovered in species richness and abundance, and in some cases their abundance exceeded those observed before the fire. A recovery in species richness after the same period was also found when examining arthopod assemblages after a fire in the Table Mountain area (Pryke & Samways 2012). Thus, ecological preferences or different life forms may determine the survival of species. The epeigaeic species (most of the Order Symphypleona) are more vulnerable to fires as they are exposed on the vegetation, while euedaphic species are deeper in the soil and may survive the fire. Recent studies using a trait-based approach have shown that species that are for example parthenogenetic and are epidaphic recover quicker after a fire than species that reproduce sexually or are euedaphic (Huebner et al. 2012, Malmström 2012). As the springtail taxonomic diversity of South Africa is only starting to be comprehended (Janion et al. 2011b), it is still unclear what the reproductive strategies are of the species found in this study. Indeed, life history traits should be explored in more detail with increasing knowledge of this group in the fynbos. For example, dispersal plays a major role in the recolonization of a site after disturbance, and for Collembola, the size of the furca has been used as a proxy for measuring dispersal. Also, it was shown in this study using springtail order as a proxy of functional group that the Symphypleona, which are usually surface dwellers (Hopkin 1997), decreased considerably in abundance and species richness immediately after the fire. However, species from the Poduromorpha was not affected as severely, as they are known to occur deeper in the soil, thus may have survived the fire. Suggestions from long-term studies indicate that surface-dwelling groups such as Symphypleona tend to be more severely affected by fire than other groups, but gradually recover over time (Malmström 2012).

Springtail abundance and species richness varied between the different study sites. The availability of refugia such as stones, deeper soils and moist litter layers, may play a vital role in the re-colonisation of species. The *Protea* site had refugia sites where litter accumulated after the fire (Supplementary material, Fig. 9). These may have provided shelter, re-colonisation sites and food availability for springtails immediately after the fire, enabling them to feed and reproduce. Similar observations were made for ants, spiders, centipedes and crickets (Pryke & Samways 2012). Yet, specialised and restricted species may be eliminated by more intense fires (Brand 2002). Another factor that may contribute to the quick recovery rate of springtails may be linked to the resilience (i.e. the ability to return to the pre-fire state equilibrium) of the plants. The resilience of plants in the fynbos biome is dependent on their life history strategies (Keeley 1986, van Wilgen & Forsyth 1992). Sprouters such as *Protea nitida* (which dominated in our Protea site) can survive fires and are not severely affected by fires (depending on the severity), while non-sprouters (reseeders) such as Ericaceae rely on seed banks to regenerate. Thus, the *Erica* site takes longer to return to its original state before the fire, while the *Protea* site recovered quicker (Supplementary material).

In a study done in the fynbos it was found that there is a strong relationship between plant stoichiometry (C/N or C/P-ratios), and decomposition rate (Bengtsson et al. 2012), and that *Galenia* litter had the highest decomposition rate, while *Restio* had the lowest decomposition rate. Due to the large variation in decomposition rates found, it has been suggested that nutrient cycling may be most important immediately after fire, when soil nutrient levels are higher (Stock & Lewis 1986). Here, litter type did not have a significant effect on Collembola species richness, but on abundance, it is important to keep this is mind when decomposition and diversity studies are undertaken.

Perhaps most significant in the context of comparisons with previous investigations of fire impacts on invertebrates (e.g. Chambers & Samways 1998, Parr et al. 2002, Parr et al. 2004, Pryke & Samways 2012), is the ability here to identify the richness and turnover contributions to change. Adoption of Carvalho et al.'s (2012) method to disaggregate the beta diversity index made this possible. The outcome revealed clearly that what was changing over the course of the study, and especially immediately following the fire, was species identity, rather than richness. In other words, the fire had significant effects on some species, but not others (see also Fig. 8). Thus, although the springtail fauna overall is resilient, clearly some species are affected more than are others, resulting in substantial turnover at the species level. Just what traits underlie this turnover is not clear, but the current data lend themselves to further trait-based investigations (see e.g. Chown 2012), to determine the extent to which effect and response traits differ (Naeem & Wright 2003). More generally, these outcomes show the significance of understanding not only that species richness and abundance are affected, but also the identity of the species present, hence emphasizing the need for studies that focus more closely at the species level, rather than simply on changes in higher taxonomic groups.

Conclusions

This study has shown that springtails are highly resilient to fire in the fynbos of South Africa. The springtails investigated here are similar in this respect to savannah ants (Parr et al. 2004) and, so far as can be ascertained from the higher taxonomic level data, to multiple groups of arthropods in the Table Mountain area (Pryke & Samways 2012). Usually fires in the fynbos have a return time of between seven and 29 years (van Wilgen & McDonald 1992, van Wilgen et al. 2010), but fynbos can burn between 4 and 6 years after the previous fire in high rainfall areas such as Jonkershoek (van Wilgen & Hensbergen 1992). Also, the frequency of fires is increasing due to human disturbances (Syphard et al. 2009). However, studies on a larger scale are needed before generalisations can be made. I recommend that future research on the well documented large scale fire plots in South Africa, such as exist in the Kruger National Park (Biggs et al. 2003), using springtails as model organisms is needed, given their important role in nutrient recycling (Rusek 1998, Hopkin 1997). With the predicted changes in landscape use and biodiversity greatest for Mediterranean climate-type ecosystems (Sala et al. 2000, Rouget et al. 2003), understanding of the response of soil fauna to disturbances such as fire is essential, especially since recent studies on decomposition rates suggest that the role of springtails in decomposition might be more important than previously thought (Bengtsson et al. 2011, 2012). Therefore, the establishment of long-term fire experiments for understanding the interactions between fire, soil fauna and decomposition would repay the investment required.

Scope of contribution of the candidate

Writing and analyses was done by the candidate.

References

Allsopp, N. (1999) Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. *Plant Ecology* **142**, 179-187.

Bengtsson, J., Janion, C., Chown, S.L. & Leinaas, H.P. (2011) Variation in decomposition rates in the fynbos biome, South Africa: the role of plant species and plant stoichiometry. *Oecologia* **165**, 225-235.

Bengtsson, J., Janion, C., Chown, S.L. & Leinaas, H.P. (2012) Litter decomposition in the fynbos vegetation, South Africa. *Soil Biology & Biochemistry* **47**, 100-105.

Biggs, R., Biggs, H.C., Dunne, T.T., Govender, N. & Potgieter, A.L.F. (2003) Experimental burn plots in the Kruger National Park: history, experimental design and suggestion for data analysis. *Koedoe* **36**, 1-15.

Block, W. (1966) Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods. *Oikos* **17**, 1-9.

Bocock, K.L. & Gilbert, O.J.W. (1957) The disappearance of leaf litter under different woodland conditions. *Plant and Soil* **9**, 179–185.

Bond, W.J. (1997) Fire. In: R.M. Cowling, D.M. Richardson & S.M. Pierce (Eds), *Vegetation of Southern Africa*, Cambridge University Press, Cambridge, pp. 421-446.

Bond, W.J. & Keeley, J.E. (2005) Fire as a global herbivore: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**, 378-394.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist* **165**, 525–538.

Bond, W.J. & van Wilgen, B.W. (1996) *Fire and Plants*. Chapman & Hall, London.

Brand, R.H. (2002) The effect of prescribed burning on epigeic springtails (Insecta: Collembola) of woodland litter. *American Midland Naturalist* **148**, 383-393.

Bretfield, G. (1999) *Synopses on Palaearctic Collembola, Volume 2, Symphypleona*. W. Dunger (Ed). Staatliches Museum für Naturkunde, Görlitz.

Carvalho, J.C., Cardoso, P. & Gomes, P. (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography* **21**, 760-771.

Chambers, B. Q. & Samways, M. J. (1998) Grasshopper response to a 40 year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodiversity and Conservation* **7**, 985–1012.

Chown, S.L. (2012) Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. *Philosophical Transactions of the Royal Society B* **367**, 1615-1627.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edition. Plymouth Marine Laboratory, UK: PRIMER-E Ltd.

Colwell, R.K. (2009) EstimateS – statistical estimation of species richness and shared species from samples. V8.20. http://viceroy.eeb.uconn.edu/EstimateSPages/EstimateS.flx.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical transactions of the Royal Society of London B* **345**, 101-118.

Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd, Chichester.

DAISIE (2009) *Handbook of alien species in Europe*. Invading Nature: Springer Series in Invasion Ecology, Volume 3. J.A. Drake (Ed). Springer. Dordrecht.

Dean, W.R.J. (1987) Birds associating with fire at Nylsvley Nature Reserve, Transvaal. *Ostrich* **58**, 103-106.

Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J. & Lavelle, P. (2006) The values of soil animals for conservation biology. *European Journal of Soil Biology* **42**, S23-S38.

de Kock, A.E., Giliomee, J.H., Pringle, K.L. & Majer, J.D. (1992) The influence of fire, vegetation age and Argentine ants (*Iridomyrmyx humilis*) on ant communities on Swartboskloof. In: *Fire in South African Mountain Fynbos. Ecosystem, Community and Species Response at Swartboskloof*. B.W. van Wilgen, D.M. Richardson, D.M., Kruger, F.J. & van Hensbergen (Eds.), pp. 203-215.

Donnelly D. & Giliomee J. H. (1985) Community structure of epigaeic ants in a pine plantation and in newly burnt fynbos. *Journal of the Entomological Society of South Africa* **48**, 259–65.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* **1**, 488-494.

Ferrar, P. (1982) Termites of a South African savannah. III. Comparative attack on toilet roll baits in subhabitats. *Oecologia* **52**, 139-146.

Fjellberg, A. (1998) *Fauna Entomologica Scandinavica Volume 35. The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha*. Brill, Leiden.

Fjellberg, A. (2007) *Fauna Entomologica Scandinavica Volume 42. The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona*. Brill, Leiden.

Fontaine, J.B. & Kennedy, P.L. (2012) Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecological Applications* **22**, 1547-1561.

Forsyth, G.G. & van Wilgen, B.W. (2010) The recent fire history of Table Mountain National Park and implications for fire management. *Koedoe* **50**, 3-9.

Fraser, M.W. (1990) Small mammals, birds and ants as seed predators in the post-fire mountain fynbos. *South African Journal of Wildlife Research* **20**, 52-56.

Gandar, M.W. (1982) Description of a fire and its effects in the Nylsvley Nature Reserve, a synthesis report. South African National Scientific Programmes Report No. 63. CSIR, Pretoria.

Goldammer, J.G. & Price, C. (1998) Potential impacts of climate change on fire regimes in the tropics based on MAGICC and a GISS GCM-derived lightning model. *Climatic Change* **39**, 273-296.

Greenslade, P. & Smith, D. (2010) Short term effects of wild fire on invertebrates in coastal heathland in southeastern Australia. *Pacific Conservation Biology* **16**, 123-132.

Gunderson, L.H. (2000) Ecological resilience – in theory and application. *Annual Review in Ecology and Systematics* **31,** 425-39.

Hansen, J., Sato, M. & Ruedy, R. (2012) Perception of climate change. *Proceedings of the National Academy of Sciences of the United States of America* **109**, E2145-E2423.’

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* **6**, 324-337.

Hugo-Coetzee, E.A. & Avenant, N.L. (2011) The effect of fire on soil oribatid mites (Acari: Orabatida) in a South African grassland. *Zoosymposia* **6**, 210-220.

Holling, C.S. (1973) Resilience and stability of ecosystems. *Annual Review in Ecology and Systematics* **4**, 1-13.

Hopkin, S. (1997) *Biology of the Springtails. Insecta: Collembola*. Oxford University Press, Oxford.

Hopkin, S. (2007) *A Key to the Collembola (Springtails) of Britain and Ireland*. FSC, London.

Huebner, K., Lindo, Z. & Lechowicz, M.J. (2012) Post-fire succession of collembolan communities in a northern hardwood forest. *European Journal of Soil Biology* **48**, 59-65.

Janion, C., Bedos, A, Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, Liu, A., Malmström, A., Porco, D., and Chown, S.L. (2011a) Springtail diversity in South Africa. *South African Journal of Science* **107**, Article #582, 7 pages.

Janion, C, Bedos, A., Deharveng, L. (2011b) The genus *Ectonura*, Cassagnau 1980 in South Africa (Collembola: Neanuridae: Neanurinae), with a key to South African Neanurinae. *ZooKeys* **136**, 31-45.

Janion, C., D'Haese, C. and Deharveng, L. (2012) A new species and first record of the genus *Triacanthella* Schaffer, 1897 (Collembola, Hypogastruridae) for Africa. *Zookeys* **163**, 57-68.

Keeley, J.E. (1986) Resilience of Mediterranean shrub communities to fire. In: *Resilience on Mediterranean-type ecosystems.* B. Dell, A.J.M. Hopkins, B.B. Lamont (Eds). Pp. 95-112, Junk, Doordrecht.

Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Taylor, S., Watson, S.J., Clarke, M.F. & Bennett, A.F. (2012) Managing fire mosaics for small mammal conservation: a landscape perspective. *Journal of Applied Ecology* **49,** 412-421.

Lach, L., Parr, C.L. & Abbott, K.L. (Eds) (2009). *Ant Ecology.* Oxford University Press, Oxford.

Laurance, W.F., Useche, W.F., Rendeiro, J. et al. (2012) Averting biodiversity collapse in tropical forests in protected areas. *Nature* **489**, 290-294.

Liu, A., Janion, C. & Chown, S.L. (2012) Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations. *Pedobiologia* **55**, 203-209.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology* **83**, 689-702.

Macfadyen, A. (1953) Notes on methods for the extraction of small soil arthropods. *Journal of Animal Ecology* **22**, 65-77.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Oxford.

Malmström, A. (2012) Life-history traits predict recovery patterns in Collembola species after fire: A 10 year study. *Applied Soil Ecology* **56**, 35-42.

Malmström, A., Persson, T., Ahlström, K., Gongalsky, K.B. & Bengtsson, J. (2009) Dynamics of soil meso- and macrofauna during a 5-year period after clear-cut burning in a boreal forest. *Applied Soil Biology* **43**, 61-74.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: biodiversity synthesis*. World Resource Institute, Washington, DC.

Naeem S. & Wright J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**, 567-579.

O'Hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution* **1**, 118-122.

Parr, C.L. & Andersen, A.N. (2008) Fire resilience of ant assemblages in long-unburnt savanna of northern Australia. *Austral Ecology* **33**, 830-838.

Parr, C.L., Bond, W.J. & Robertson, H.G. (2002) A preliminary study of the effects of fire on ants (Formicidae) in South African savannah. *African Entomology* **10**, 101-111.

Parr, C. L. & Chown, S.L. (2003) A burning issue for conservation: A critique of faunal fire research in Southern Africa. *Austral Ecology* **28**, 384-395.

Parr, C. L., Robertson, H.G., Biggs, H.C. & Chown, S.L. (2004) Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* **41**, 630-642.

Pastro, L.A., Dickman, C. R. & Letnic, M. (2011) Burning for biodiversity or burning biodiversity? Prescribed burning vs. wildfire impacts on plants, lizards and mammals. *Ecological Applications* **21**, 3238-3253.

Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* **1**, 6-18.

Pflug, A. & Wolters, V. (2001) Influence of drought and litter age on Collembola communities. *European Journal of Soil Biology* **37**, 305-308.

Pierce, J.L., Meyer, G.A. & Jull, A.J.T. (2004) Fire-induced erosion and millennial-scale change in northern ponderosa pine forests. *Nature* **432**, 87-90.

Pimm, S.L. (1991) *The Balance of Nature*. The University of Chicago Press, London.

Potapov, M. (2001) *Synopses on Palaearctic Collembola, Volume 3, Isotomidae*. W. Dunger, W. (Ed). Staatliches Museum für Naturkunde, Görlitz.

Potapov, M., Janion, C. and Deharveng, L. (2011) Two new species of *Parisotoma* (Collembola: Isotomidae) from the Western Cape, South Africa. *Zootaxa* **2771**, 17-24.

Pryke, J.S. & Samways, M.J. (2012) Importance of using many taxa and having adequate controls for monitoring impacts of fire for arthropod conservation. *Journal of Insect Conservation* **16**, 177-185.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L. & Rutherford, M.C. (2006) Fynbos Biome. In: *The Vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia* 19, pp. 52-219. L. Mucina & M.C. Rutherford (eds.) South African National Biodiversity Institute, Pretoria.

Renschin, M.L., Thompson, L.C. & Shelton, M.G. (2004) Long-term prescribed burning regime has little effect on springtails in pine stands of southern Arkansas. In: *Proceedings of the 12th biannual southern silvicultural research conference.* Connor. Kristina, F. (Ed), pp. 79-81. Department of Agriculture, Forest Service, Southern Research Station NC: U.S.

Rignot, E., Mouginot, J. & Scheuchl, B. (2011) Ice flow of the Antarctic sheet. *Science* **333**, 1427-1430.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* **112**, 63-85.

Rusek, J. (1998) Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation* **7**, 1207-1219.

Sla, O.E., Chapin III, F.S., Armesto, J.J. et al. (2000) Global biodiversity scenarios for 2100. *Science* **287**, 1770-1774.

Smucker, K.M., Hutto, R.L. & Steele, B.M. (2005) Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* **15**, 1535-1549.

Stock, W.D. & Lewis, O.A.M. (1986) Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *Journal of Ecology* **74**, 317-328.

Stocks, B. J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin J-Z., Lawrence, K., Hartley, G.R, Mason, J.A., & McKenney, D.W. (1998) Climate Change and Forest Fire Potential in Russian and Canadian Boreal Forests. *Climatic Change* **38**, 1-13.

Sutherland, E.F. & Dickman, C.R. (1999) Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* **26**, 405-419.

Syphard, A.D., Radeloff, V.C., Hawbaker, T.J. & Stewart, S.I. (2009) Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conservation Biology* **23**, 758-769.

van Wilgen, B.W. (2009) The evolution of fire and invasive alien plant management practices in fynbos. *South African Journal of Science* **105**, 335-342.

van Wilgen, B.W., Forsyth, G.G., De Klerk, H., Das, S., Khuluse, S. & Schmitz, P. (2010) Fire management in Mediterranean-climate shrublands: A case study from the Cape fynbos, South Africa. *Journal of Applied Ecology* **47**, 631-638.

van Wilgen, B.W. & Forsyth, G.G. (1992) regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In: *Fire in South African Mountain Fynbos: Ecosystem, Community and Species Response at Swartboskloof.* B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen (Eds), pp. 54-80. Springer-Verlag, Berlin.

van Wilgen, B.W., Govender, N, Forsyth, G.G. & Kraaij, T. (2011) Towards adaptive fire management for biodiversity conservation: Experience in South African National parks. *Koedoe* **53**, art # 982, 9 pages.

van Wilgen, B.W. & Hensbergen, H.J. (1992) Fuel properties of vegetation in Swartboskloof. In: *Fire in South African Mountain Fynbos: Ecosystem, Community and Species Response at Swartboskloof.* B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen (Eds), pp. 37-53. Springer-Verlag, Berlin.

van Wilgen, B.W. & McDonald, D.J. (1992) The Swartboskloof Experimental Site. In: *Fire in South African Mountain Fynbos: Ecosystem, Community and Species Response at Swartboskloof.* B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen (Eds), pp. 1-20. Springer-Verlag, Berlin.

Vasconcelos, H.L., Pacheco, R., Silva, R.C., Vasconcelos, P.B., Lopes, C.T., Costa, A.N. & Bruna, E.M. (2009) Dynamics of leaf-litter arthropod fauna following fire in a neotropical woodland savanna. *PloS One* **4**, e7762.

Versfeld, D.B., Richardson, D.M., Van Wilgen, B.W., Chapman, R.A. & Forsyth, G.G. (1992) The Climate of Swartboskloof. In: *Fire in South African Mountain Fynbos: Ecosystem, Community and Species Response at Swartboskloof.* B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen (Eds), pp. 21-35. Springer-Verlag, Berlin.

Vorster, C. (2011) Distribution and bait preference of Argentine ant in natural vegetation. MSc Thesis, Stellenbosch University.

Wardle, D.A. (2002) *Communities and Ecosystems. Linking the aboveground and belowground components*. Princeton University Press, Princeton.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629-1633.

Tables

Table 1: Species richness, abundance and species richness estimator values for springtails (2008 = pre-fire, 2009-2011 = post-fire, n=58).

	2008	**2009**	**2010**	**2011**
Total abundance	3871	4905	14486	18994
Total species richness	25	26	26	27
Jacknife 2 (no re-sampling)	31.9	29.95	30.9	30.95
Jacknife 2 (with re-sampling)	25.96 ± 3.99	26.03 ± 3.72	26.45 ± 2.96	27.79 ± 3.5

Table 2: Mean species richness (SR) and abundance of springtails in each site in Jonkershoek Nature Reserve, (2008 = pre-fire, 2009-2011 = post-fire, n=30).

	2008		**2009**		**2010**		**2011**	
	Erica	***Protea***	***Erica***	***Protea***	***Erica***	***Protea***	***Erica***	***Protea***
SR	5.73 ± 0.20	8.97 ± 3.22	3.87 ± 0.30	7.00 ± 0.37	6.93 ± 0.43	7.67 ± 0.36	4.87 ± 0.33	6.77 ± 0.38
Abundance	79.97 ± 16.31	49.03 ± 8.37	71.83 ± 0.84	91.67 ± 1.99	427.14 ± 125	69.37 ± 9.45	416.6 ± 144.05	230.47 ± 87.05

Table 3: List of springtail species and their total abundance per year, (2008 = pre-fire, 2009-2011 = post-fire, n=60 per year).

Species	**2008**	**2009**	**2010**	**2011**
Triacanthella sp.	248	98	717	5942
Austrogastrura sp.	6	0	175	30
Ectonura sp.	9	15	1	1
Hypogastrura sp.	1	0	0	0
Aethiopella sp.	2	2	9	7
cf. Tasmanura sp.	2	0	1	0
Afrodontella sp.	2	5	2	0
Pseudochorutes sp.	18	21	21	18
Ceratophysella sp.	0	2	0	0
Xenylla sp.	0	8	0	3
Mesaphorura sp.	47	41	37	37
Tullbergia sp.	2	92	116	32
Brachystomella sp.	297	38	76	561
Setanodosa sp.	0	0	0	1
Lepidocyrtus sp.	167	438	141	461
Pseudosinella sp.	0	2	0	1
cf. Sinella sp.	11	2	0	0
Isotomurus sp.	24	65	117	6
Isotoma sp.	11	0	558	3
Parisotoma sp.	2502	2588	707	416
cf. Folsomina sp.	0	1	0	0
Cryptopygus sp.	136	1278	10416	20067
C. caecus sp.	149	105	74	15
cf. Proisotoma sp.	0	0	544	53
Folsomides sp.	0	44	0	0
Seira sp.1	31	31	381	174
Seira sp.2	6	7	121	18
Seira sp.3	20	11	21	26

Seira sp.4	0	0	53	20
Sminthurinus sp.1	129	6	147	39
Sminthurinus sp.2	18	0	13	17
Bourletiellidae sp.	5	0	4	3
Arrhopalites sp.	0	1	2	7
Sphaeridia sp.	28	2	32	29
Megalothorax sp.	0	2	0	0

Table 4: Outcome of generalized linear models investigating the effect of year, litter type and site on species richness and abundance for (A) both *Protea* and *Erica* sites, (B) *Erica* site and (C) *Protea* site (***p<0.001, ** p<0.01, *p<0.05, ns = not significant).

(A)

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Site *Protea*	-0.0058	0.0802	-0.073	ns
Year 2009	-0.3939	0.0893	-4.413	***
Year 2010	0.1200	0.0770	2.593	*
Year 2011	-0.1438	0.0839	-1.713	ns
Site *Protea* x Year 2009	0.5993	0.1176	5.098	***
Site *Protea* x Year 2010	0.0968	0.1075	0.901	ns
Site *Protea* x Year 2011	0.3153	0.1140	2.767	**
Abundance				
Litter *Galenia*	1.1073	0.2828	3.916	***
Litter *Restio*	0.6726	0.2999	2.242	*
Site *Protea*	-0.8119	0.2148	-3.780	***
Year 2009	0.2367	0.4400	0.538	ns
Year 2010	1.3541	0.3703	3.656	***
Year 2011	1.6022	0.3609	4.439	***

(B) *Erica* site

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Year 2009	-0.3939	0.0919	-4.287	***
Year 2010	0.1999	0.0793	2.519	***
Year 2011	-0.1438	0.0864	-1.665	ns
Abundance				
Litter *Galenia*	1.0472	0.4071	2.573	*
Litter *Restio*	0.8237	0.4172	1.975	ns
Year 2009	-0.1073	0.7094	-0.151	ns
Year 2010	1.6892	0.5332	3.168	**
Year 2011	1.6329	0.5343	3.056	**

(C) *Protea* site

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Year 2009	0.20544	0.07425	2.767	**
Year 2010	0.29642	0.07279	4.072	***
Year 2011	0.17154	0.07483	2.293	*
Abundance				
Litter *Galenia*	1.2426	0.3029	4.103	***
Litter *Restio*	0.2621	0.3549	0.738	ns
Year 2009	0.6250	0.4126	1.515	ns
Year 2010	0.3462	0.4351	0.796	ns
Year 2011	1.5469	0.3667	4.218	***

Table 5: Outcome of generalized linear models showing the significant factors when investigating the effect of year, litter type and site on species richness and abundance for (A) Order Poduromorpha, (B) Order Entomobryomorpha, and (C) Order Symphypleona, (***p<0.001, ** p<0.01, *p<0.05, ns = not significant).

A) Poduromorpha

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Site *Protea*	0.04383	0.06549	0.669	ns
Litter *Galenia*	0.01856	0.08022	0.231	ns
Litter *Restio*	0.10936	0.07824	1.398	ns
Year	0.2968	0.0302	9.814	***
Abundance				
Site *Protea*	-0.5350	0.2473	-2.163	*
Litter *Galenia*	1.2174	0.3365	3.618	***
Litter *Restio*	0.7993	0.3548	2.253	*
Year	0.7430	0.1322	5.619	***

B) Entomobryomorpha

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Site *Protea*	-6.732e-03	5.441e-02	-0.124	ns
Litter *Galenia*	9.324e-03	6.677e-02	0.140	ns
Litter *Restio*	1.317e-01	6.463e-02	2.038	*
Year	1.913e-01	2.467e-02	7.753	***
Abundance				
Litter *Galenia*	1448.8510	651.9559	-2.222	*
Litter *Restio*	657.0384	656.4251	-1.001	ns
Year	0.1708	0.2602	0.656	ns
Litter *Galenia* x Year	0.7213	0.3244	2.224	*
Litter *Restio* x Year	0.3273	0.3266	1.002	ns

c) Symphypleona

	Estimate	s.e.	t-value	p
Species richness				
Site *Protea*	0.07001	0.07352	0.952	ns
Litter *Galenia*	0.01311	0.09073	0.144	ns
Litter *Restio*	0.13519	0.08784	1.539	ns
Year	0.35968	0.03445	10.441	***
Abundance				
Site *Protea*	-0.5387	0.2512	2.145	*
Litter *Galenia*	1.2274	0.3428	3.580	***
Litter *Restio*	0.8130	0.3611	2.252	*
Year	0.7801	0.1368	5.703	***

Figures

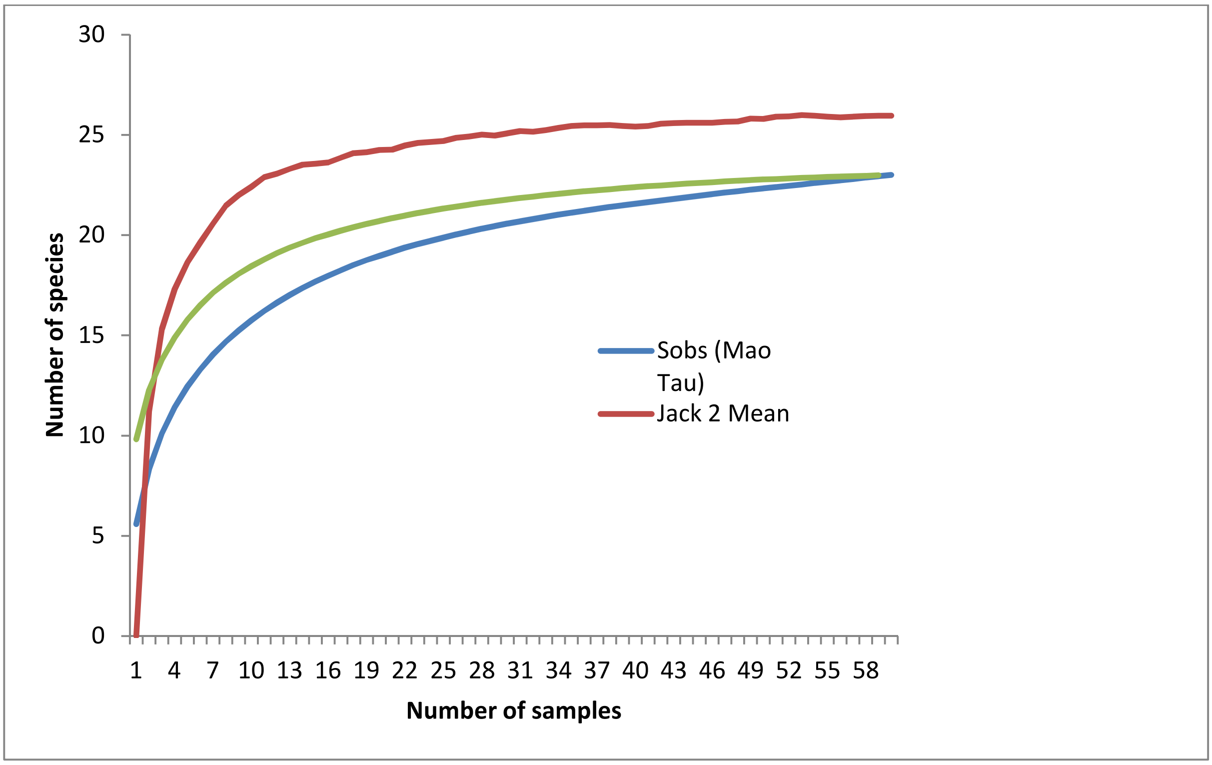


Fig 1A: Species accumulation curves for 2008 (pre-fire).

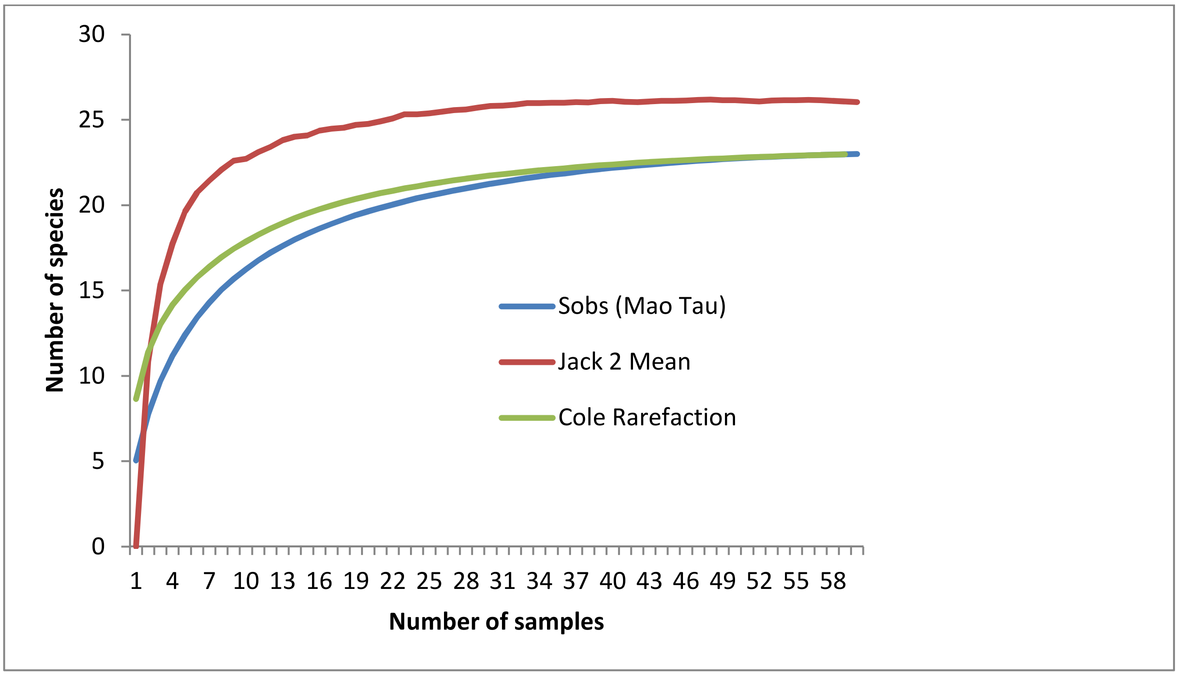


Fig 1B: Species accumulation curves for 2009.

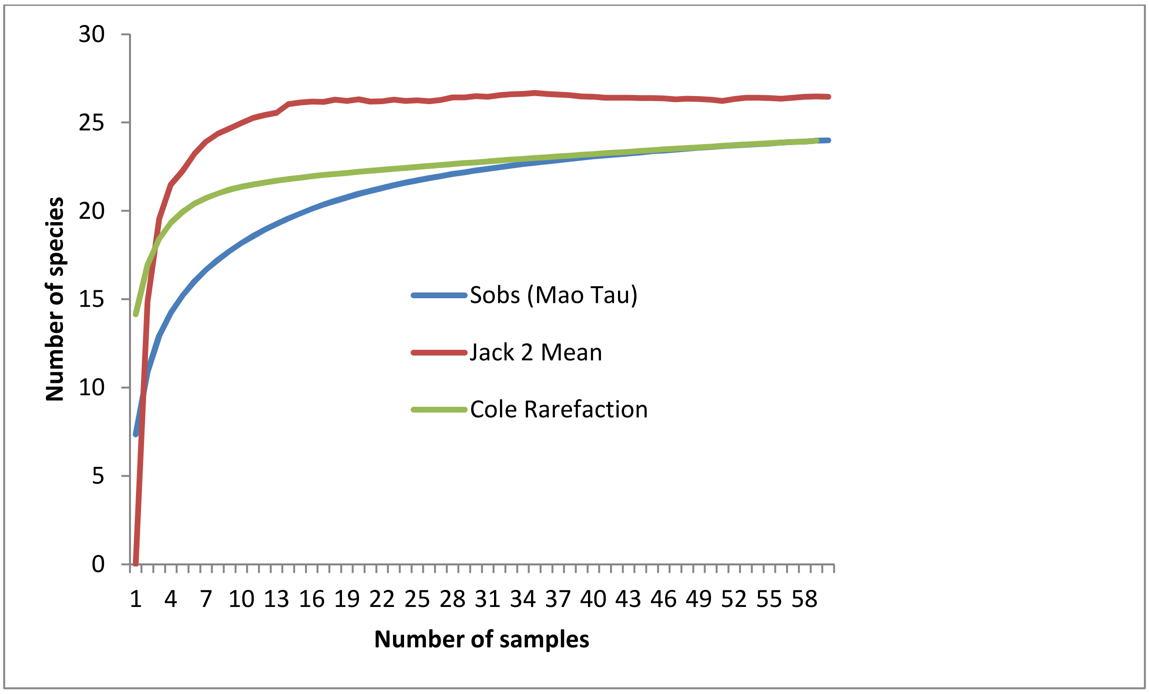


Fig 1C: Species accumulation curves for 2010.

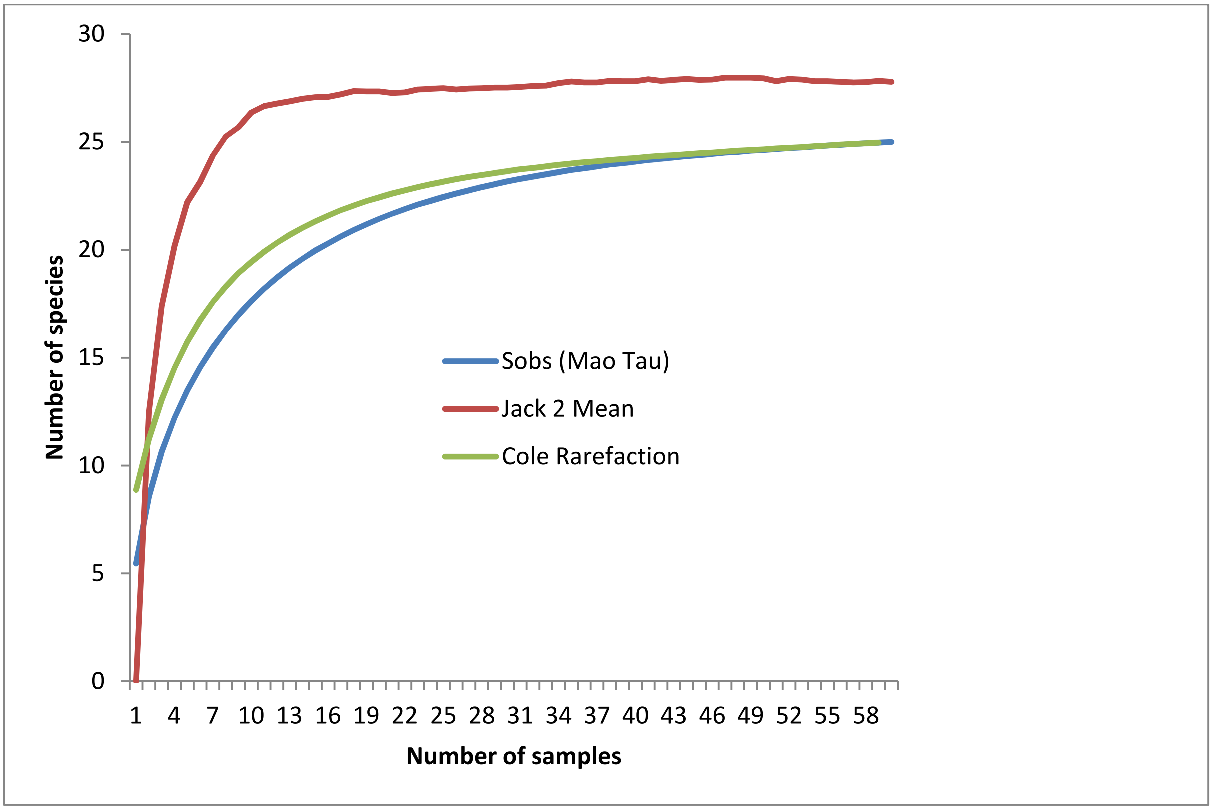


Fig1D: Species accumulation curves for 2011.

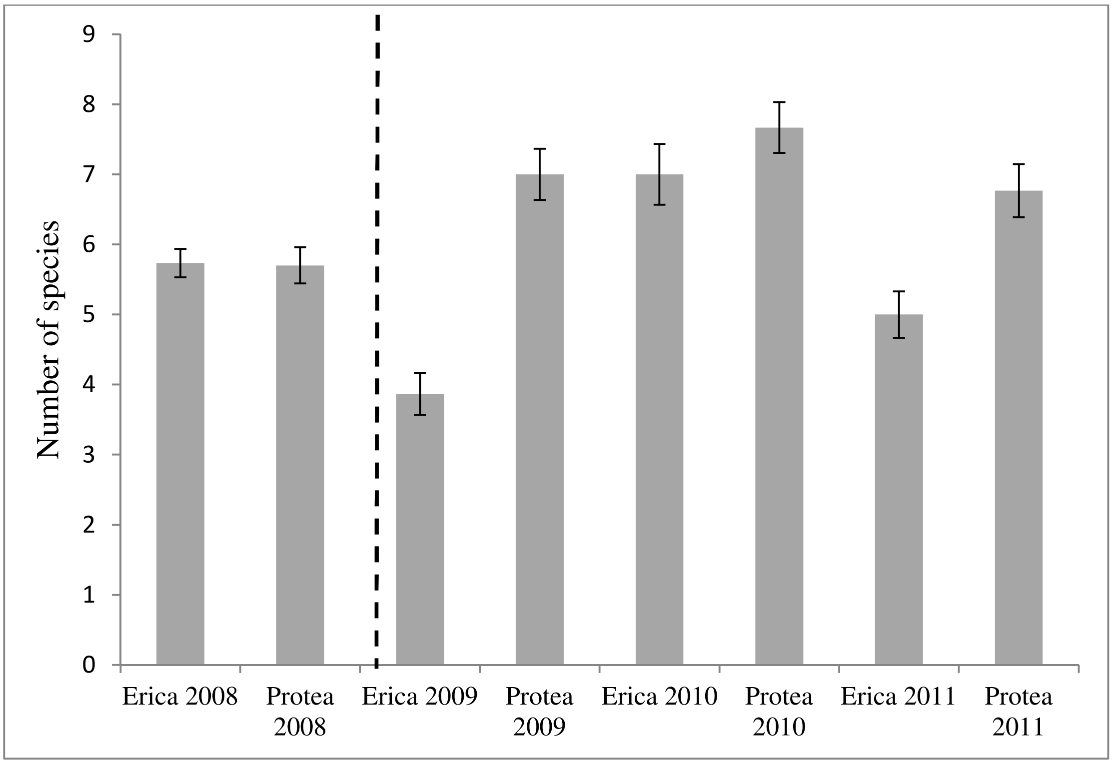


Fig 2: Mean number of species (per litterbag) in different sites over the period of study. The dashed line indicates the fire event (error bars indicate standard error).

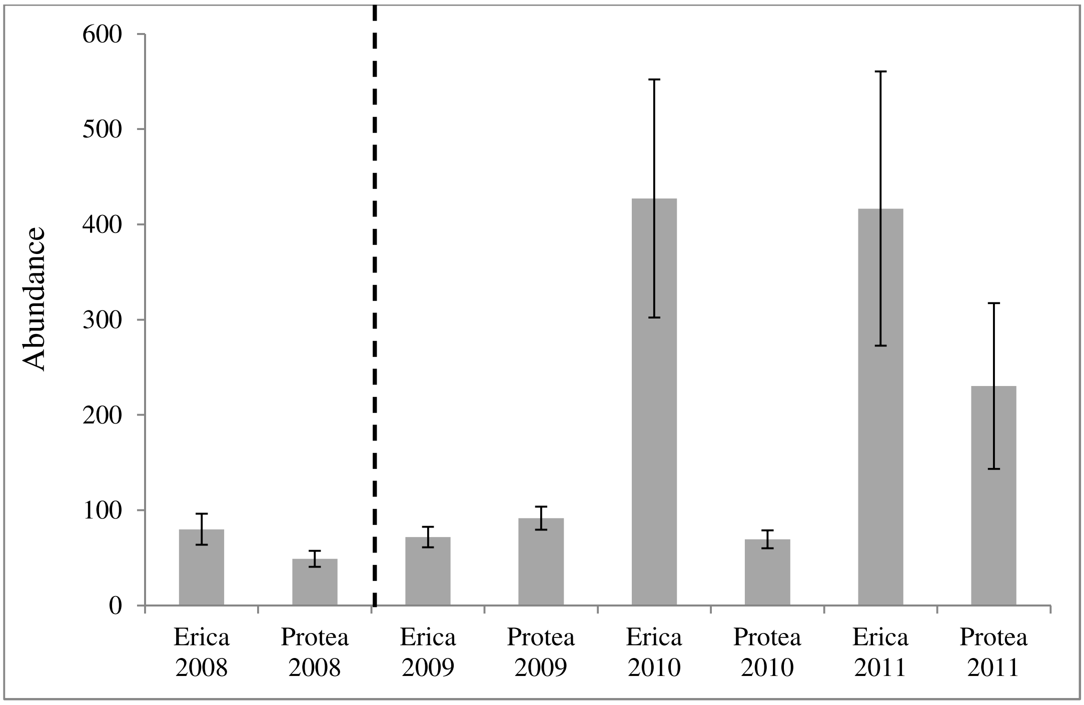


Fig 3: Mean abundance (per litterbag) in different sites over the period of study. The dashed line indicates the fire event (error bars indicate standard error).

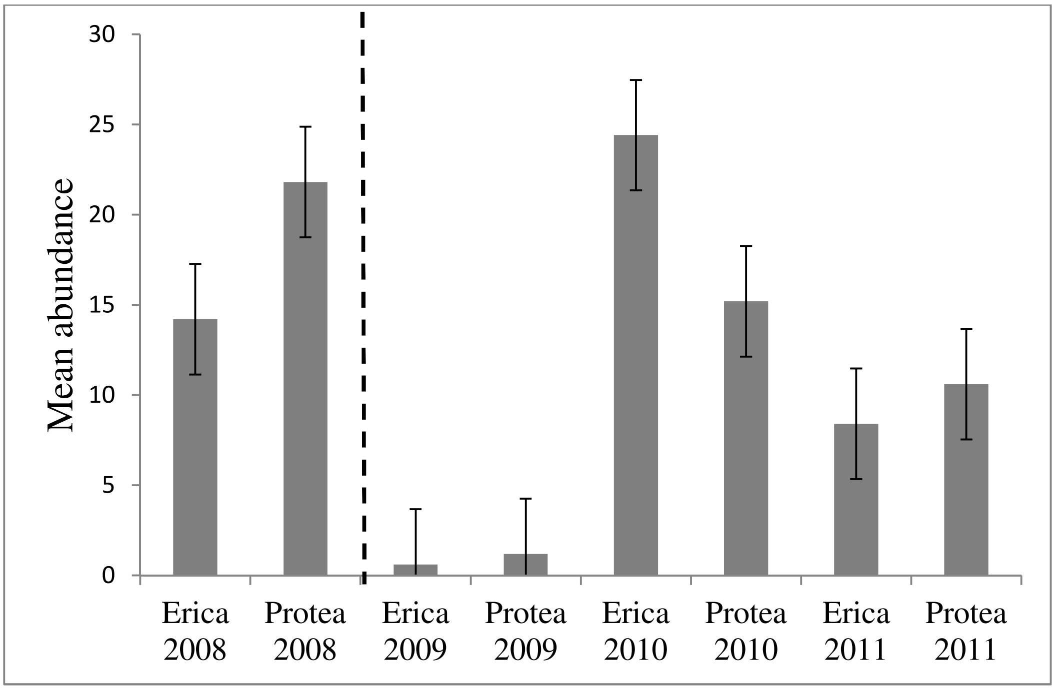


Fig. 4A: The mean abundance (per litterbag) of the order Symphypleona. The dashed line indicates the fire event, (error bars indicate standard error).

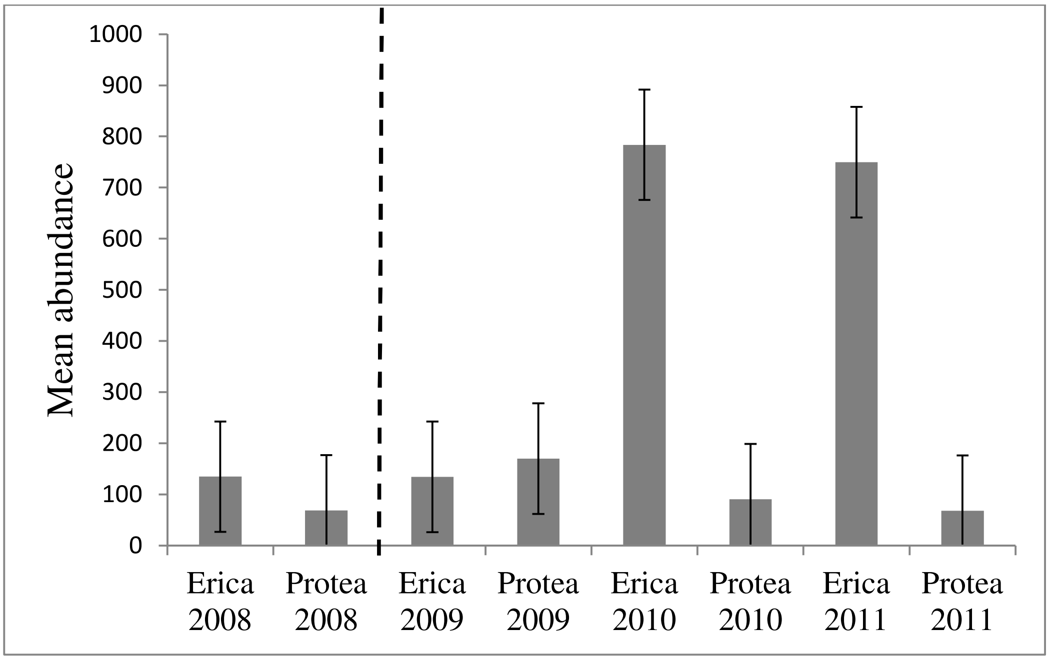


Fig. 4B: The mean abundance (per litterbag) of the order Entomobryomorpha. The dashed line indicates the fire event, (error bars indicate standard error).

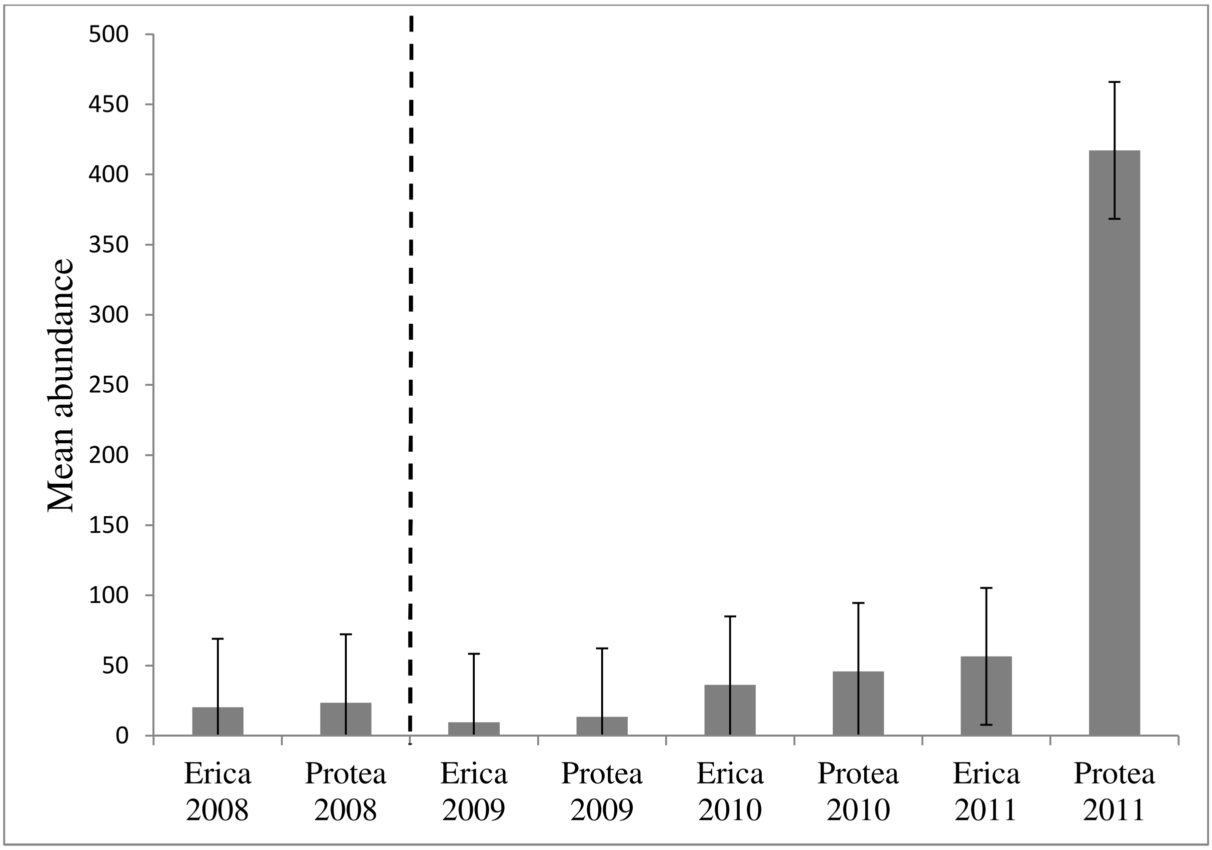


Fig. 4C: The mean abundance (per litterbag) of the order Poduromorpha. The dashed line indicates the fire event, (error bars indicate standard errors).

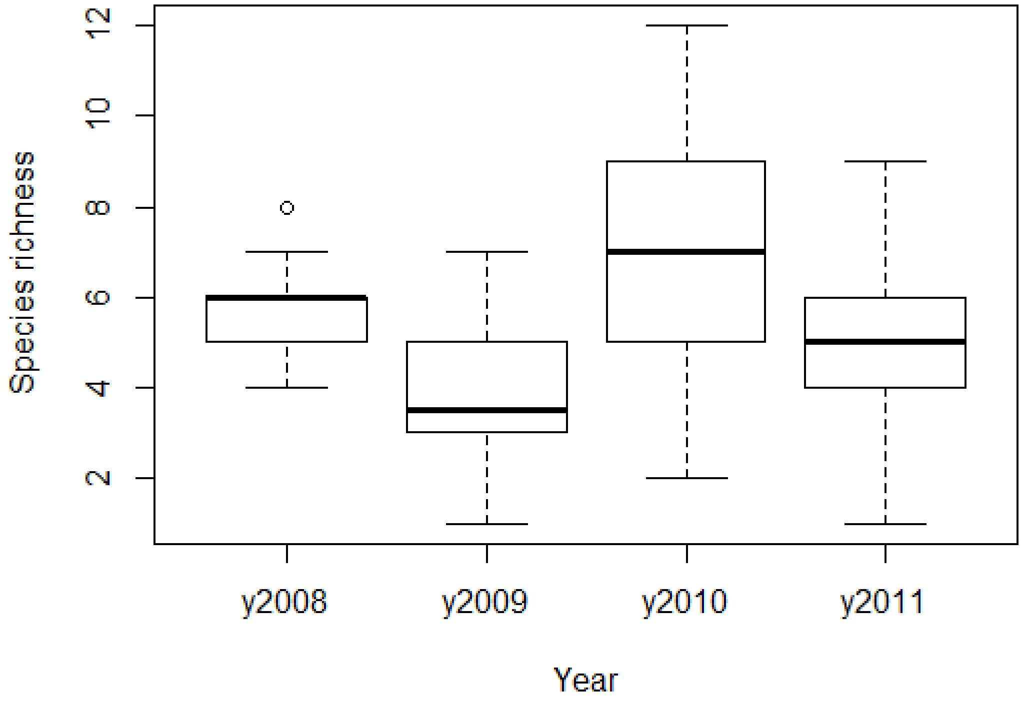


Fig. 5A: Species richness per year in the *Erica* site. Bars indicate mean ± S.E, outliers shown as open circles.

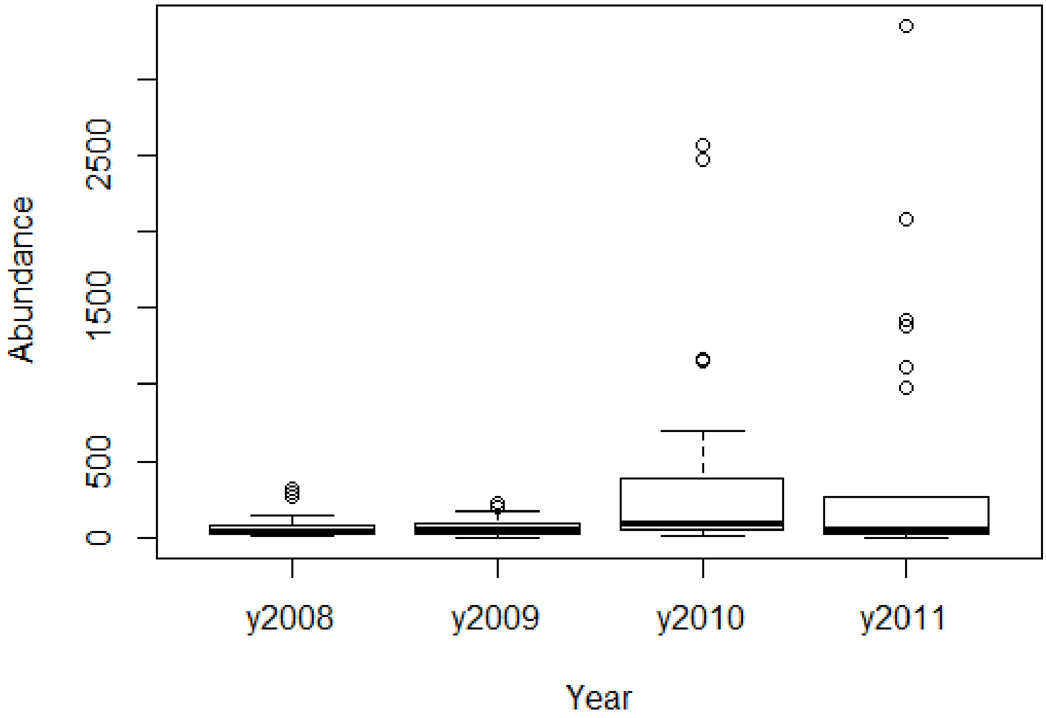


Fig. 5B: Collembola abundance per year in the *Erica* site. Bars indicate mean ± S.E, outliers shown as open circles.

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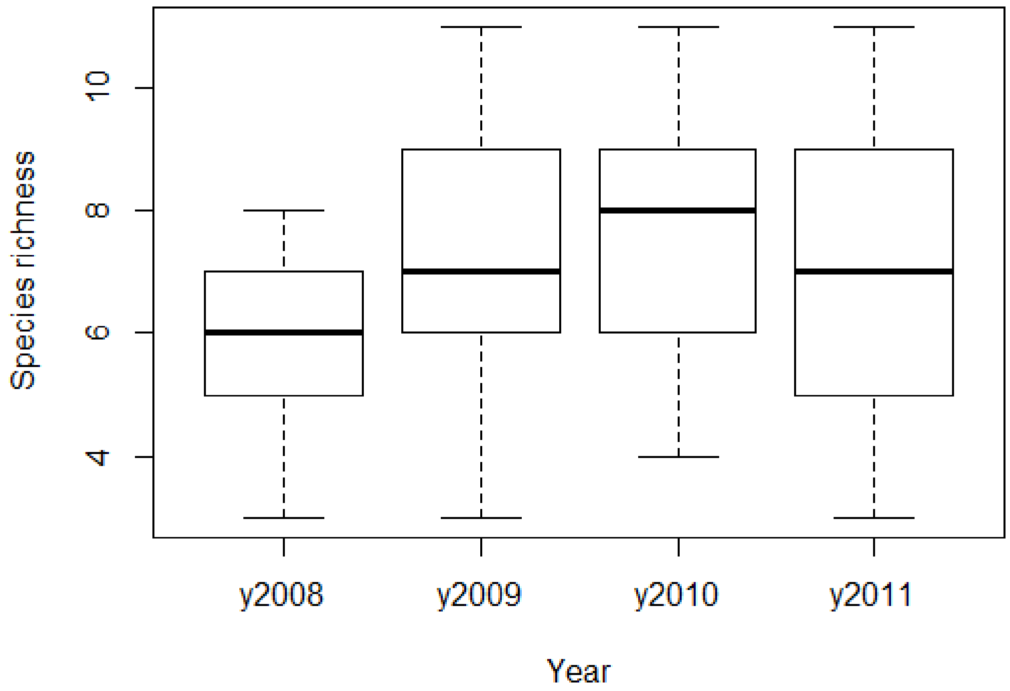

Fig. 5C: Mean species richness per year in the *Protea* site. Bars indicate mean ± S.E.

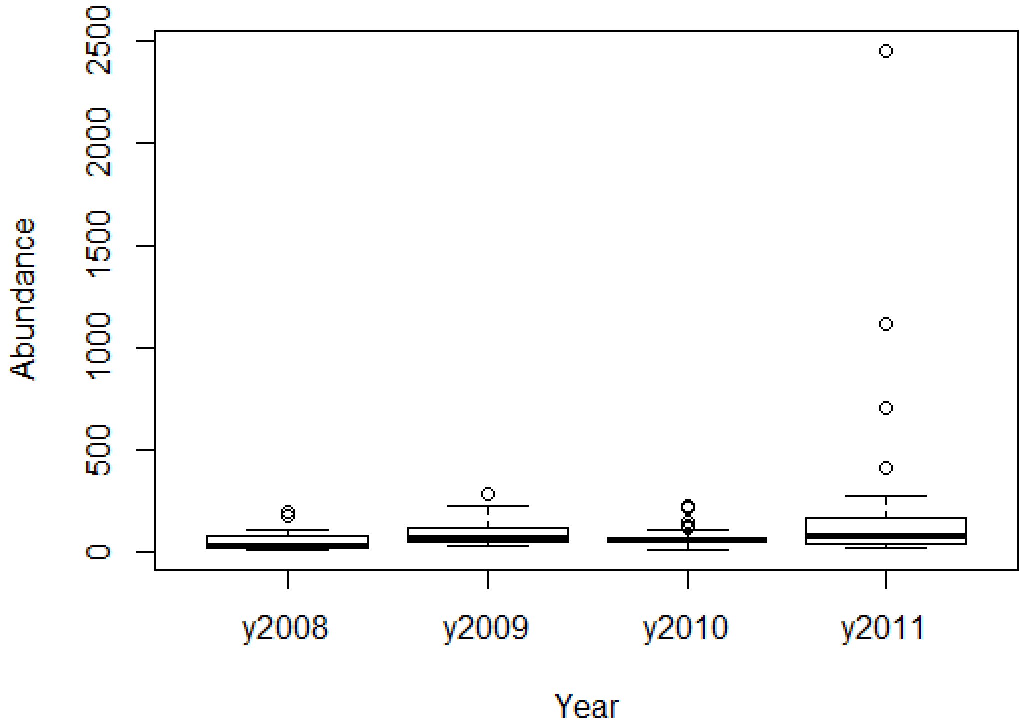

Fig. 5D: Mean abundance per year in the *Protea* site. Bars indicate mean ± S.E., outliers shown as open circles.

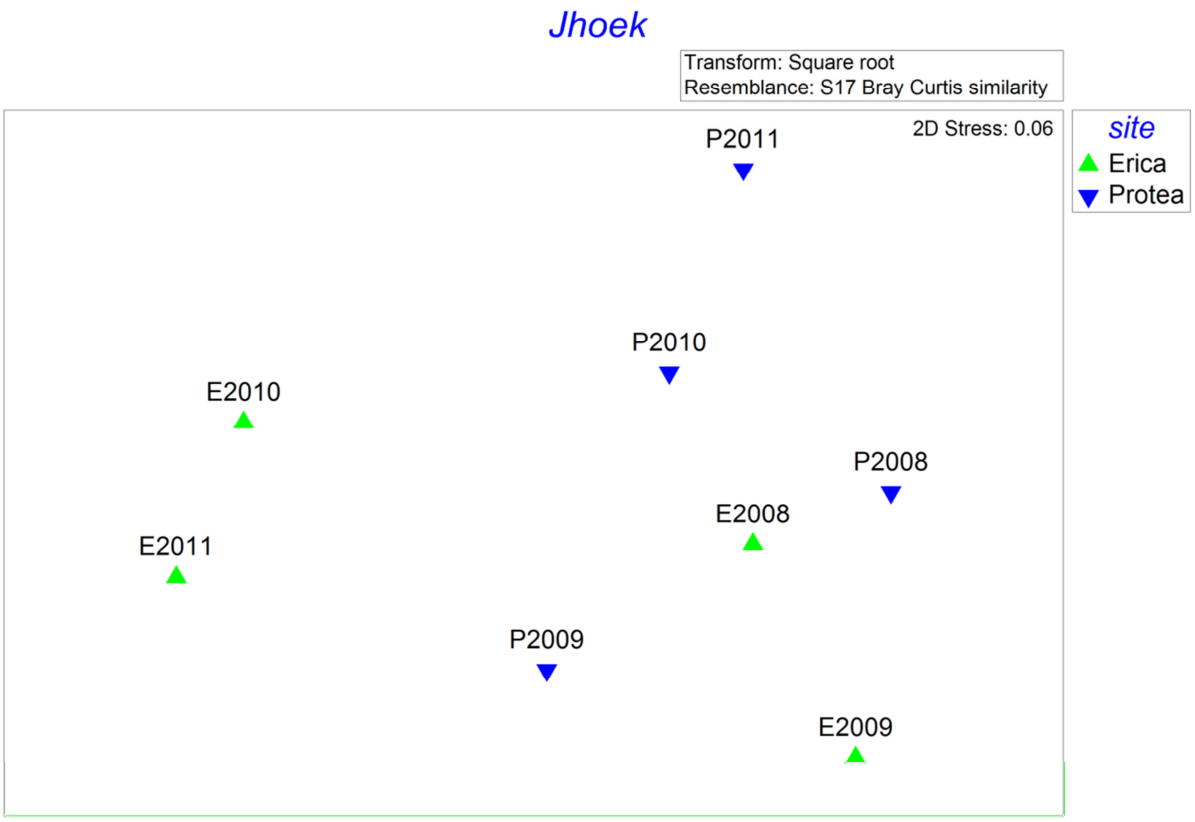

Fig 6A: Non-metric ordination plots of springtail assemblages in the *Erica* (E) and *Protea* (P) sites pre-fire (2008) and one, two and three years after the fire (2009, 2010 and 2011) using square root transformed abundance data.

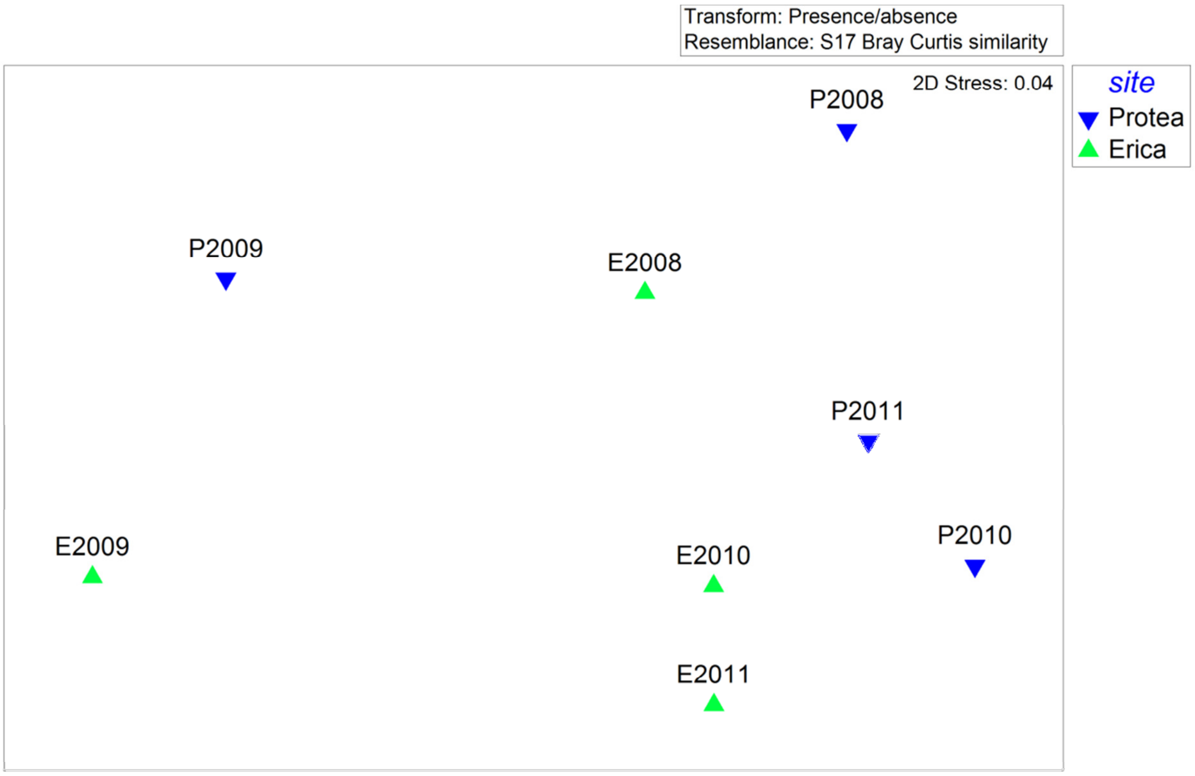

Fig 6B: Non-metric ordination plots of springtail assemblages in the *Erica* (E) and *Protea* (P) sites pre-fire (2008) and one, two and three years after the fire (2009, 2010 and 2011) using presence-absence data.

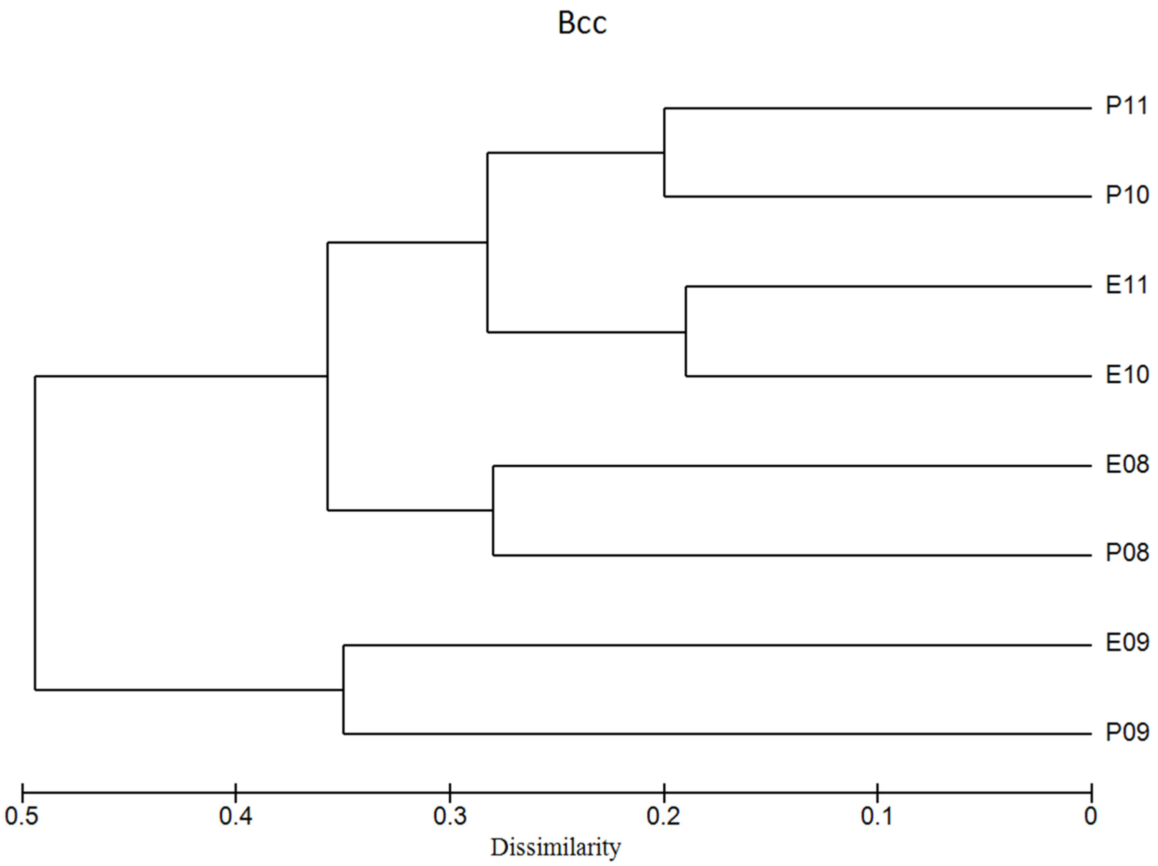

Figure 7A: Dendrogram of B_{cc}, E=*Erica* site, P=*Protea* site, before the fire (08) and one (09), two (10) and three (11) years after the fire. An increase in branch length indicates an increase in dissimilarity.

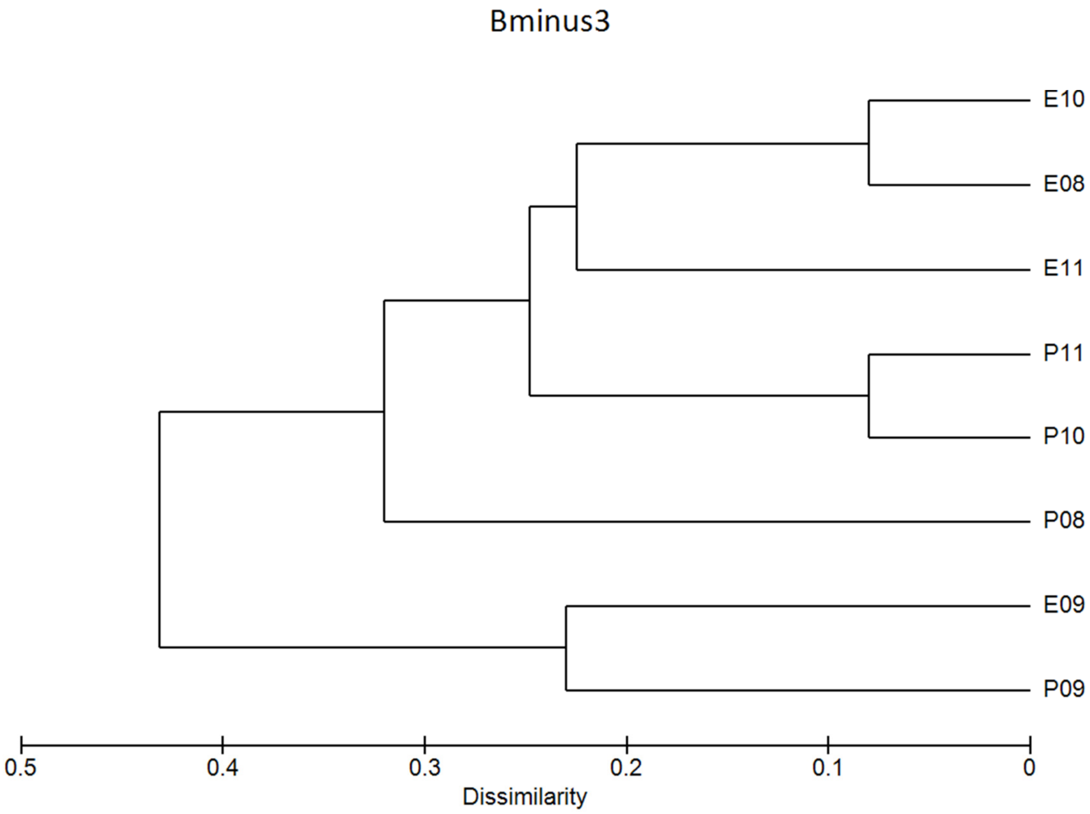

Figure 7B: Dendrogram of B_{-3}, E=*Erica* site, P=*Protea* site, before the fire (08) and one (09), two (10) and three (11) years after the fire. An increase in branch length indicates an increase in dissimilarity.

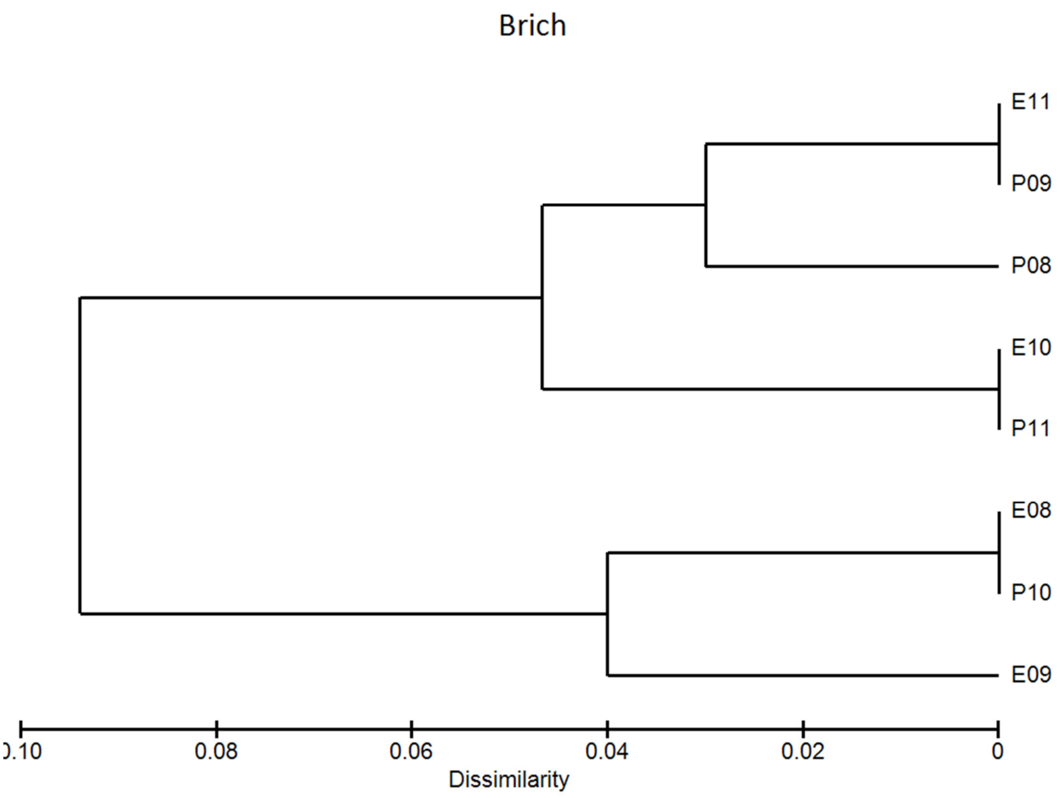

Figure 7C: Dendrogram of B_{rich}, E=*Erica* site, P=*Protea* site, before the fire (08) and one (09), two (10) and three (11) years after the fire. An increase in branch length indicates an increase in dissimilarity.

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Species	Protea2008	Protea2009	Protea2010	Protea2011	Erica2008	Erica2009	Erica2010	Erica2011
Triacanthella	■	■	■	■	■	■	■	■
Mesaphorura	■	■	■	■	■	■	■	■
Lepidocyrtus	■	■	■	■	■	■	■	■
Brachystomella	■	■	■	■	■	■	■	■
Isotomurus	■	■	■	■	■	■	■	■
Parisotoma	■	■	■	■	■	■	■	■
Cryptopygus	■	■	■	■	■	■	■	■
C. caecus	■	■	■	■	■	■	■	■
Seira sp. 1	■	■	■	■	■	■	■	■
Sminthurinus sp. 1	■	■	■	■	■	■	■	■
Seira sp. 2	■	■	■	■	■		■	■
Pseudochorutes	■		■	■	■	■	■	■
Tullbergia		■	■	■	■	■	■	■
Seira sp. 3	■	■			■	■	■	■
Sphaeridia	■	■		■	■		■	■
Austrogastrura	■		■	■			■	■
Isotoma			■	■	■		■	■
Ectonura	■	■	■	■	■			
Bourletiellidae	■		■	■	■		■	
Aethiopella	■	■	■	■				
Afrodontella		■			■	■	■	
Xenylla		■		■		■		■
Seira sp. 4			■	■			■	■
cf. Sinella	■	■				■		
cf. Proisotoma			■	■			■	■
Sminthurinus sp. 2	■			■	■		■	■
Arrhopalites			■			■	■	■
cf. Tasmanura	■				■		■	
Pseudosinella		■		■		■		
Folsomides		■				■		
Megalothorax						■		
cf. Folsomina		■						
Setanodosa								■
Ceratophysella		■						
Hypogastrura	■							

Figure 8: A presence-absence matrix of springtail species in Jonkershoek Nature Reserve. Species are displayed in columns and the different years and sites in rows. Filled squares indicate species presences.

Supplementary material

Table 1:
Results from a SIMPER analysis using square-root transformed abundance data.

2008 vs. 2009
Average dissimilarity = 63.44

	2008	**2009**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Parisotoma sp.	5.02	5.64	14.12	1.31	22.26	22.26
Cryptopygus sp.	0.85	3.29	10.2	1.07	16.07	38.34
Lepidocyrtus sp.	1.28	1.97	5.86	1.15	9.23	47.57
Triacanthella sp.	1.12	0.7	4.79	0.81	7.55	55.12
Brachystomella sp.	1.46	0.33	4.46	0.95	7.03	62.16
C. caecus	0.84	0.66	3.92	0.76	6.17	68.33
Sminthurinus sp.	1.06	0.09	3.69	1.01	5.81	74.14
Mesaphorura sp.	0.4	0.4	2.33	0.74	3.67	77.81
Tullbergia sp.	0.02	0.58	1.96	0.56	3.09	80.9
Seira sp. 1	0.33	0.3	1.7	0.67	2.68	83.58
Pseudochorutes	0.22	0.26	1.44	0.61	2.28	85.85
Isotomurus	0.18	0.25	1.27	0.41	2	87.86
Folsomides	0	0.41	1.18	0.52	1.87	89.72
Seira sp. 3	0.21	0.14	1.08	0.5	1.71	91.43

2008 vs. 2010
Average dissimilarity = 73.39

	2008	**2010**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	0.85	7.47	13.05	0.68	17.79	17.79
Parisotoma sp.	5.02	2.3	10.7	1.15	14.58	32.37
Triacanthella sp.	1.12	1.53	5.6	0.74	7.63	40
Seira sp. 1	0.33	1.75	4.75	1	6.47	46.47
Isotoma sp.	0.07	1.79	4.63	0.79	6.3	52.77
Brachystomella	1.46	0.4	4.51	0.92	6.14	58.91
Sminthurinus sp. 1	1.06	0.97	3.54	1.1	4.82	63.74
Lepidocyrtus	1.28	1.19	3.31	1.05	4.51	68.24
C. caecus	0.84	0.44	3.04	0.72	4.14	72.39
Austrogastura	0.06	0.88	2.87	0.58	3.92	76.3
Seira sp. 2	0.08	0.85	2.85	0.72	3.88	80.19
Tullbergia sp.	0.02	0.66	2.12	0.51	2.88	83.07
Mesaphorura sp.	0.4	0.35	1.9	0.71	2.58	85.65
cf. Proisotoma	0	0.7	1.78	0.24	2.43	88.08
Seira sp. 4	0	0.55	1.64	0.67	2.23	90.31

2009 vs. 2010

Average dissimilarity = 72.73

	2009	**2010**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	3.29	7.47	16.24	0.86	22.33	22.33
Parisotomasp.	5.64	2.3	11.76	1.25	16.17	38.49
Triacanthella sp.	0.7	1.53	4.69	0.66	6.45	44.94
Isotoma sp.	0	1.79	4.64	0.78	6.38	51.32
Seira sp. 1	0.3	1.75	4.49	1	6.18	57.5
Lepidocyrtus	1.97	1.19	4.12	1.02	5.66	63.16
Tullbergia sp.	0.58	0.66	2.84	0.67	3.91	67.07
Seira sp. 2	0.11	0.85	2.55	0.75	3.51	70.59
Sminthurinus sp. 1	0.09	0.97	2.53	0.87	3.48	74.07
Austrogastrura	0	0.88	2.46	0.58	3.39	77.46
C. caecus	0.66	0.44	2.46	0.68	3.38	80.84
cf. Proisotoma	0	0.7	1.9	0.24	2.61	83.45
Isotomurus sp.	0.25	0.38	1.64	0.34	2.25	85.7
Brachystomella	0.33	0.4	1.58	0.59	2.17	87.87
Seira sp. 4	0	0.55	1.56	0.64	2.15	90.02

2008 vs. 2011

Average dissimilarity = 73.55

	2008	**2011**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	0.85	8.16	14.56	0.71	19.8	19.8
Triacanthella sp.	1.12	5.07	13.18	0.86	17.91	37.71
Parisotoma sp.	5.02	1.67	11.9	1.11	16.18	53.89
Brachystomella sp.	1.46	1.3	5.54	1	7.53	61.42
Lepidocyrtus	1.28	2.03	5.49	1.03	7.46	68.88
Seira sp. 1	0.33	0.89	3.3	0.68	4.48	73.36
Sminthurinus sp. 1	1.06	0.41	3.22	0.95	4.38	77.74
C. caecus	0.84	0.16	2.74	0.61	3.73	81.47
Mesaphoruras sp.	0.4	0.19	1.62	0.51	2.2	83.67
Sminthurinus sp. 2	0.21	0.26	1.37	0.68	1.86	85.53
Sphaeridia sp.	0.22	0.21	1.27	0.44	1.73	87.25
Pseudochorutes sp.	0.22	0.25	1.26	0.59	1.71	88.97
Seira sp. 3	0.21	0.17	1.04	0.44	1.41	90.38

2009 vs. 2011

Average dissimilarity = 71.52

	2009	**2011**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	3.29	8.16	18.24	0.9	25.5	25.5
Parisotoma sp.	5.64	1.67	13.81	1.18	19.31	44.81
Triacanthella sp.	0.7	5.07	11.02	0.8	15.41	60.22

Lepidocyrtus sp.	1.97	2.03	3.79	0.93	5.3	65.52
Brachystomella sp.	0.33	1.3	3.61	0.68	5.05	70.56
Seira sp. 1	0.3	0.89	2.97	0.61	4.15	74.72
C. caecus	0.66	0.16	2.12	0.6	2.96	77.68
Tullbergia sp.	0.58	0.26	2.04	0.61	2.85	80.53
Mesaphorura sp.	0.4	0.19	1.49	0.5	2.08	82.61
Pseudochorutes sp.	0.26	0.25	1.38	0.66	1.93	84.54
Sminthurinus sp. 1	0.09	0.41	1.3	0.57	1.82	86.36
Folsomides sp.	0.41	0	1.02	0.49	1.43	87.79
Seira sp. 3	0.14	0.17	0.91	0.39	1.27	89.06
Seira sp. 4	0	0.26	0.87	0.44	1.21	90.27

2010 vs. 2011

Average dissimilarity = 69.95

	2010	**2011**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Cryptoygus sp.	7.47	8.16	16.04	0.77	22.93	22.93
Triacantella sp.	1.53	5.07	11.67	0.81	16.68	39.61
Parisotoma sp.	2.3	1.67	4.82	0.9	6.89	46.51
Seira sp. 1	1.75	0.89	4.5	1.01	6.43	52.93
Isotoma sp. 1	1.79	0.05	4.11	0.75	5.87	58.81
Lepidocyrtus sp.	1.19	2.03	3.99	0.94	5.7	64.51
Brachystomella sp.	0.4	1.3	2.91	0.65	4.15	68.66
Sminthurinus sp. 1	0.97	0.41	2.5	0.93	3.57	72.23
Austrogastrura	0.88	0.19	2.5	0.59	3.57	75.8
Seira sp. 2	0.85	0.16	2.48	0.74	3.55	79.34
Tullbergia sp.	0.66	0.26	2.1	0.55	3	82.34
cf. Proisotoma sp.	0.7	0.23	2.07	0.29	2.96	85.29
Seira sp. 4	0.55	0.26	1.66	0.75	2.37	87.66
C. caecus	0.44	0.16	1.33	0.49	1.9	89.56
Isotomurus sp.	0.38	0.09	1.24	0.3	1.77	91.33

***Erica* site**

Average similarity: 35.28

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	8.52	13.62	0.92	38.6	38.6
Parisotoma sp.	3.1	11.88	0.73	33.67	72.27
Triacanthella sp.	1.23	1.73	0.4	4.91	77.18
Lepidocyrtus sp.	0.74	1.65	0.41	4.69	81.87
Brachystomella sp.	0.88	1.13	0.36	3.19	85.06
Isotoma sp.	0.67	1.05	0.34	2.97	88.03
Seira sp. 1	0.66	0.99	0.34	2.81	90.84

***Protea* site**

Average similarity: 46.25

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Parisotoma sp.	4.22	16.08	1.58	34.77	34.77
Lepidocyrtus sp.	2.49	10.36	1.4	22.41	57.18
Triacanthella sp.	2.99	5.28	0.52	11.41	68.59
Cryptopygus sp.	1.37	3.1	0.54	6.71	75.3
Sminthurinus sp. 1	0.76	2.23	0.49	4.82	80.12
Brachystomella sp.	0.86	2.17	0.44	4.69	84.81
Seira sp. 1	0.98	1.82	0.47	3.93	88.74
C. caecus	0.67	1.12	0.36	2.42	91.16

Erica vs. Protea

Average dissimilarity = 70.20

	Erica	***Protea***				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	8.52	1.37	16.06	0.87	22.88	22.88
Parisotoma sp.	3.1	4.22	10.44	1.16	14.87	37.75
Triacanthella sp.	1.23	2.99	8.14	0.7	11.6	49.35
Lepidocyrtus sp.	0.74	2.49	6.54	1.17	9.32	58.67
Brachystomella sp.	0.88	0.86	3.56	0.73	5.07	63.74
Seira sp. 1	0.66	0.98	3.02	0.77	4.31	68.05
C. caecus	0.37	0.67	2.71	0.64	3.86	71.91
Sminthurinus sp. 1	0.5	0.76	2.42	0.8	3.45	75.36
Mesaphorura sp.	0.32	0.36	1.75	0.61	2.49	77.85
Tullbergia sp.	0.44	0.32	1.69	0.53	2.4	80.25
Isotoma sp.	0.67	0.29	1.58	0.41	2.25	82.5
Austrogastrura sp.	0.06	0.51	1.32	0.42	1.87	84.37
Pseudochorutes sp.	0.25	0.24	1.31	0.62	1.87	86.24
Seira sp. 2	0.2	0.4	1.29	0.53	1.84	88.08
Isotomurus sp.	0.25	0.2	1.22	0.35	1.73	89.81
cf. Proisotoma sp.	0.44	0.03	1.13	0.22	1.6	91.42

Table 2:

Results from a SIMPER analysis using presence-absence data.

2008 vs. 2009

Average dissimilarity = 57.19

	2008	2009				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Sminthurinus sp. 1	0.6	0.08	5.33	1.09	9.32	9.32
Cryptopygus sp.	0.43	0.82	5.24	1.07	9.16	18.48
Brachystomella sp.	0.63	0.22	5.08	1.03	8.88	27.36
Triacanthella sp.	0.43	0.4	4.54	0.92	7.95	35.31
C. caecus	0.38	0.32	3.95	0.81	6.91	42.22
Mesaphorura sp.	0.23	0.27	3.74	0.79	6.54	48.76
Lepidocyrtus sp.	0.68	0.67	3.66	0.72	6.41	55.16
Seira sp. 1	0.23	0.2	2.94	0.69	5.15	60.31
Tullbergia sp.	0.02	0.3	2.82	0.64	4.93	65.24
Pseudochorutes sp.	0.17	0.2	2.71	0.64	4.73	69.97
Folsomides sp.	0	0.27	2.05	0.59	3.58	73.55
Seira sp. 3	0.15	0.12	2.03	0.53	3.55	77.1
Isotomurus sp.	0.12	0.08	1.77	0.46	3.09	80.19
Ectonura sp.	0.08	0.15	1.64	0.49	2.87	83.06
Sminthurinus sp. 1	0.15	0	1.47	0.41	2.56	85.62
Seira sp. 2	0.07	0.1	1.32	0.41	2.31	87.93
Parisotoma sp.	0.97	0.93	1.12	0.31	1.95	89.88
Sphaeridia sp.	0.12	0.02	1.06	0.37	1.86	91.74

2008 vs. 2010

Average dissimilarity = 62.13

	2008	2010				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Brachystomella sp.	0.63	0.17	4.78	1.18	7.7	7.7
Isotoma sp.	0.03	0.61	4.57	1.15	7.35	15.05
Seira sp. 1	0.23	0.66	4.55	1.13	7.32	22.37
Sminthurinus sp. 1	0.6	0.53	4.03	0.96	6.49	28.86
Triacanthella sp.	0.43	0.44	3.88	0.95	6.24	35.1
Seira sp. 2	0.07	0.46	3.6	0.89	5.8	40.9
Cryptopygus sp.	0.43	0.73	3.52	0.86	5.66	46.56
C. caecus	0.38	0.2	3.21	0.8	5.17	51.73
Parisotoma sp.	0.97	0.61	3.21	0.74	5.16	56.9
Lepidocyrtus sp.	0.68	0.69	3.08	0.75	4.96	61.85
Mesaphorura sp.	0.23	0.24	3.06	0.78	4.93	66.79
Austro	0.03	0.41	2.96	0.79	4.76	71.55
Seira sp. 4	0	0.37	2.68	0.75	4.32	75.87

Tullbergia sp.	0.02	0.31	2.43	0.65	3.92	79.79
Pseudochorutes sp.	0.17	0.2	2.22	0.64	3.57	83.35
Isotomurus sp.	0.12	0.14	1.72	0.5	2.77	86.12
Sminthurinus sp. 2	0.15	0.08	1.42	0.47	2.29	88.41
Seira sp. 2	0.15	0.05	1.39	0.46	2.24	90.65

2009 vs. 2010

Average dissimilarity = 63.70

	2009	**2010**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Isotoma sp.	0	0.61	5.13	1.12	8.05	8.05
Seira sp. 1	0.2	0.66	4.92	1.09	7.72	15.77
Sminthurinus sp. 1	0.08	0.53	4.19	0.98	6.57	22.34
Triacanthella sp. 1	0.4	0.44	4.11	0.91	6.45	28.79
Parisotoma sp.	0.93	0.61	3.95	0.76	6.2	34.99
Seira sp. 2	0.1	0.46	3.69	0.82	5.8	40.79
Tullbergia sp.	0.3	0.31	3.54	0.78	5.56	46.35
Cryptopygus sp.	0.82	0.73	3.19	0.7	5.01	51.36
Lepidocyrtus sp.	0.67	0.69	3.08	0.68	4.84	56.2
Austrogastrura sp.	0	0.41	2.91	0.79	4.57	60.77
C. caecus	0.32	0.2	2.83	0.71	4.43	65.21
Seira sp. 4	0	0.37	2.8	0.73	4.39	69.6
Mesaphorura sp.	0.27	0.24	2.57	0.69	4.03	73.63
Pseudochorutes sp.	0.2	0.2	2.51	0.68	3.93	77.56
Brachystomella sp.	0.22	0.17	2.5	0.67	3.92	81.48
Folsomides sp.	0.27	0	1.84	0.58	2.89	84.37
Isotomurus sp.	0.08	0.14	1.55	0.48	2.43	86.8
Seira sp. 3	0.12	0.05	1.24	0.41	1.94	88.74
Ectonura sp.	0.15	0.02	1.06	0.43	1.66	90.41

2008 vs. 2011

Average dissimilarity = 56.93

	2008	**2011**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Brachystomella sp.	0.63	0.45	4.93	1.04	8.66	8.66
Triacanthella sp.	0.43	0.74	4.85	1.02	8.52	17.18
Sminthurinus sp. 1	0.6	0.29	4.56	0.96	8	25.18
Seira sp. 4	0.23	0.41	3.96	0.88	6.96	32.14
Parisotoma sp.	0.97	0.59	3.85	0.79	6.77	38.91
C. caecus	0.38	0.1	3.65	0.81	6.41	45.32
Cryptopygus sp.	0.43	0.72	3.33	0.76	5.85	51.17
Lepidocyrtus sp.	0.68	0.66	3.3	0.71	5.8	56.97
Sminthurinus sp. 2	0.15	0.24	2.95	0.73	5.19	62.15

Pseudochorutes sp.	0.17	0.22	2.71	0.65	4.76	66.91
Mesaphorura sp.	0.23	0.12	2.61	0.62	4.59	71.5
Seira sp. 3	0.15	0.1	1.92	0.52	3.38	74.87
Sphaeridia sp.	0.12	0.14	1.85	0.52	3.26	78.13
Seira sp. 4	0	0.22	1.81	0.52	3.19	81.32
Isotomurus sp.	0.12	0.07	1.57	0.44	2.76	84.08
Tullbergia sp.	0.02	0.14	1.24	0.41	2.18	86.26
Seira sp. 2	0.07	0.09	1.18	0.39	2.07	88.33
Austrogastura sp.	0.03	0.12	1.06	0.4	1.87	90.2

2009 vs. 2011

Average dissimilarity = 59.81

Species	**2009 Av.Abund**	**2011 Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Triacanthella sp.	0.4	0.74	5.21	0.94	8.7	8.7
Parisotoma sp.	0.93	0.59	4.92	0.79	8.23	16.94
Brachystomella sp.	0.22	0.45	4.91	0.89	8.2	25.14
Cryptopygus sp.	0.82	0.72	3.7	0.72	6.18	31.32
Seira sp. 1	0.2	0.41	3.67	0.77	6.13	37.45
Tullbergia sp.	0.3	0.14	3.44	0.69	5.76	43.21
Pseudochorutes sp.	0.2	0.22	3.41	0.71	5.69	48.9
C. caecus	0.32	0.1	3.33	0.69	5.56	54.47
Lepidocyrtus sp.	0.67	0.66	3.01	0.6	5.04	59.5
Mesaphorura sp.	0.27	0.12	2.79	0.65	4.66	64.17
Sminthurinus sp. 1	0.08	0.29	2.54	0.66	4.25	68.42
Folsomides sp.	0.27	0	2.01	0.57	3.36	71.77
Seira sp. 3	0.12	0.1	1.93	0.47	3.23	75.01
Seira sp. 4	0	0.22	1.91	0.5	3.19	78.2
Sminthurinus sp. 2	0	0.24	1.83	0.53	3.06	81.25
Seira sp. 2	0.1	0.09	1.34	0.43	2.24	83.49
Sphaeridia sp.	0.02	0.14	1.31	0.4	2.18	85.67
Ectonura sp.	0.15	0.02	1.11	0.42	1.86	87.53
Isotomurus sp.	0.08	0.07	1.09	0.39	1.83	89.36
cf. Proisotoma sp.	0	0.1	1.09	0.32	1.83	91.19

2010 vs 2011

Average dissimilarity = 59.13

Species	**2010 Av.Abund**	**2011 Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Isotoma sp.	0.61	0.05	4.79	1.14	8.1	8.1
Triacanthella sp.	0.44	0.74	4.5	1.03	7.62	15.72
Seira sp. 1	0.66	0.41	4.25	0.98	7.19	22.9
Sminthurinus sp. 1	0.53	0.29	4.04	0.99	6.84	29.74
Brachystomella sp.	0.17	0.45	3.61	0.84	6.1	35.84

Seira sp. 2	0.46	0.09	3.6	0.86	6.08	41.92
Seira sp. 4	0.37	0.22	3.21	0.82	5.43	47.35
Austrogastura sp.	0.41	0.12	2.95	0.79	4.98	52.34
Tullbergia sp.	0.31	0.14	2.84	0.71	4.8	57.14
Lepidocyrtus sp.	0.69	0.66	2.75	0.67	4.65	61.78
Pseudochorutes sp.	0.2	0.22	2.54	0.67	4.3	66.08
Parisotoma sp.	0.61	0.59	2.5	0.62	4.23	70.31
Cryptopygus sp.	0.73	0.72	2.4	0.63	4.06	74.37
Mesaphorura sp.	0.24	0.12	2.26	0.64	3.82	78.19
Sminthurinus sp. 1	0.08	0.24	2.21	0.66	3.74	81.93
C. caecus	0.2	0.1	2.1	0.59	3.55	85.48
Sphaeridia sp.	0.08	0.14	1.56	0.49	2.63	88.11
Isotomurus sp.	0.14	0.07	1.44	0.46	2.44	90.55

Erica site

Average similarity: 45.75

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Cryptopygus sp.	0.84	14.25	1.3	31.15	31.15
Parisotoma sp.	0.62	10.57	0.88	23.11	54.26
Triacanthella sp.	0.46	3.59	0.48	7.85	62.11
Lepidocyrtus sp.	0.45	3.24	0.48	7.09	69.2
Brachystomella sp.	0.35	2.72	0.4	5.95	75.15
Seira sp. 1	0.3	2	0.38	4.37	79.52
Sminth sp. 2	0.31	1.96	0.38	4.27	83.79
Isotoma sp.	0.21	1.93	0.39	4.21	88
Tullbergia sp.	0.2	1.14	0.23	2.49	90.49

Protea site

Average similarity: 55.24

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Parisotoma sp.	0.93	13.47	2.17	24.39	24.39
Lepidocyrtus sp.	0.9	12.32	1.8	22.3	46.68
Triacanthella sp.	0.55	5.19	0.68	9.39	56.07
Cryptopygus sp.	0.51	4.55	0.66	8.24	64.31
Sminthurinus sp. 1	0.45	3.72	0.55	6.73	71.04
Brachystomella sp.	0.39	3.27	0.49	5.92	76.97
Seira sp.1	0.45	3	0.52	5.44	82.4
C. caecus	0.34	2	0.39	3.62	86.02
Austrogastura sp.	0.23	1.47	0.36	2.66	88.68
Seira sp. 2	0.22	1.02	0.29	1.84	90.52

***Protea* vs *Erica* site**

Average dissimilarity = 57.59

Species	***Erica*** **Av.Abund**	***Protea*** **Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Lepidocyrtus sp.	*0.45*	*0.9*	*5.09*	*1.03*	*8.83*	*8.83*
Cryptopygus sp.	*0.84*	*0.51*	*4.36*	*0.91*	*7.56*	*16.4*
Triacanthella sp.	*0.46*	*0.55*	*4.22*	*0.91*	*7.32*	*23.72*
Seira sp. 1	*0.3*	*0.45*	*3.65*	*0.82*	*6.34*	*30.05*
Brachystomella sp.	*0.35*	*0.39*	*3.6*	*0.81*	*6.25*	*36.3*
Sminthurinus sp. 1	*0.31*	*0.45*	*3.3*	*0.8*	*5.74*	*42.04*
C. caecus	*0.17*	*0.34*	*3.28*	*0.75*	*5.7*	*47.74*
Parisotoma sp.	*0.62*	*0.93*	*3.21*	*0.72*	*5.56*	*53.3*
Mesaphorura sp.	*0.19*	*0.24*	*2.97*	*0.72*	*5.16*	*58.46*
Pseudochorutes sp.	*0.21*	*0.18*	*2.77*	*0.67*	*4.8*	*63.26*
Tullbergia sp.	*0.2*	*0.18*	*2.33*	*0.6*	*4.04*	*67.3*
Seira sp. 2	*0.14*	*0.22*	*1.92*	*0.55*	*3.33*	*70.64*
Sminthurinus sp. 2	*0.13*	*0.11*	*1.7*	*0.51*	*2.95*	*73.59*
Seira sp. 3	*0.14*	*0.07*	*1.61*	*0.48*	*2.79*	*76.38*
Austrogastura sp.	*0.05*	*0.23*	*1.61*	*0.52*	*2.79*	*79.17*
Isotomurus sp.	*0.12*	*0.08*	*1.51*	*0.46*	*2.62*	*81.8*
Seira sp. 4	*0.13*	*0.17*	*1.5*	*0.48*	*2.61*	*84.4*
Sphaeridia sp.	*0.08*	*0.09*	*1.3*	*0.43*	*2.26*	*86.67*
Isotoma sp.	*0.21*	*0.13*	*1.27*	*0.44*	*2.2*	*88.86*
Ectonura sp.	*0.02*	*0.12*	*1.12*	*0.38*	*1.95*	*90.82*

Fig. 1A: Litterbag when planted in the soil.

Fig. 1B: Litterbag when removed from soil.

Fig. 2: Fire that swept through Jonkershoek Nature Reserve, February 2009, picture by J. Lee.

Fig. 3A: Erica site, March 2008.

Fig. 3B: Protea site, March 2008.

Fig. 4A: Erica site, April 2009.

Fig. 4B: Erica site, July 2009.

Fig. 5A: Protea site, April 2009.

Fig. 5B: Protea site, July 2009.

Fig. 6A: Erica site, May 2010.

Fig. 6B: Protea site, May 2010.

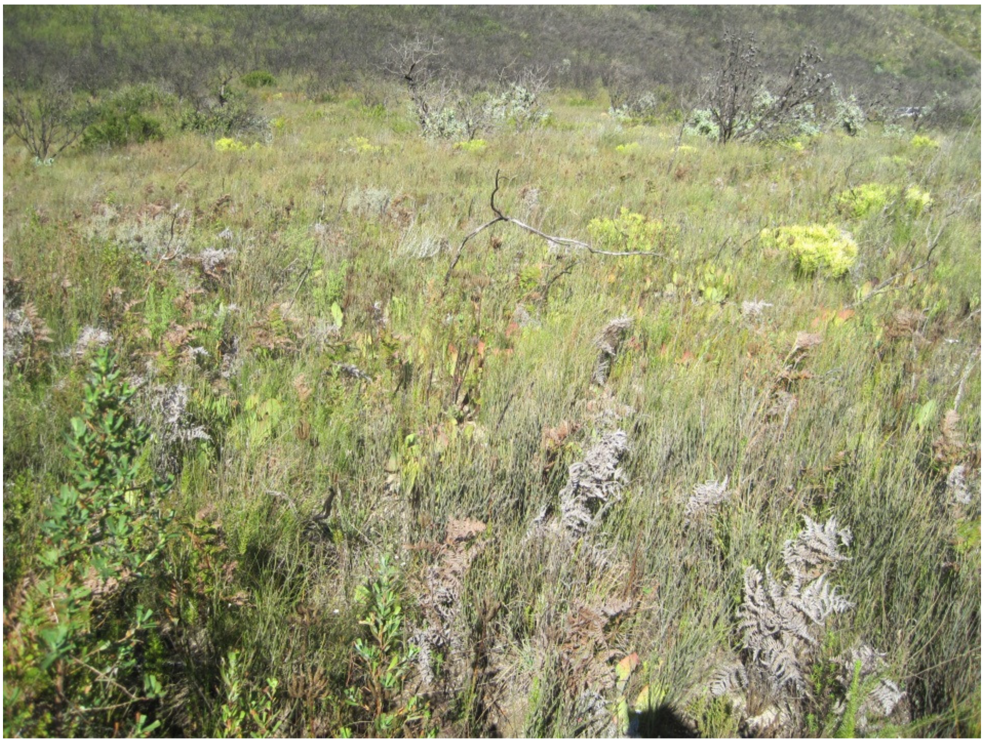


Fig 7A: Erica site, 2011

Fig. 7B: Protea site, 2011.

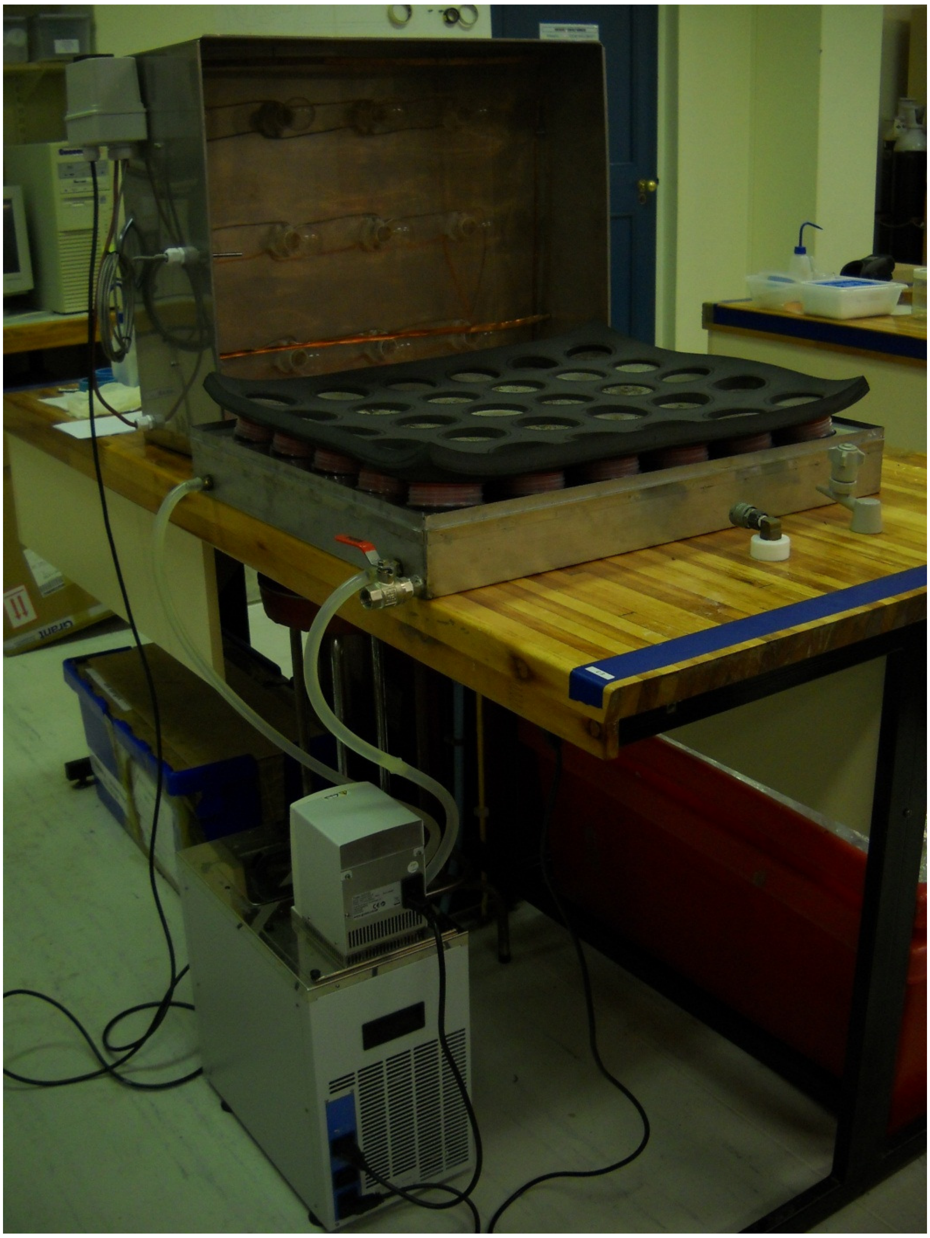


Fig. 8: High gradient extractor connected to a waterbath.

Fig. 9: An example of refugia provided by rocks in the *Protea* site.

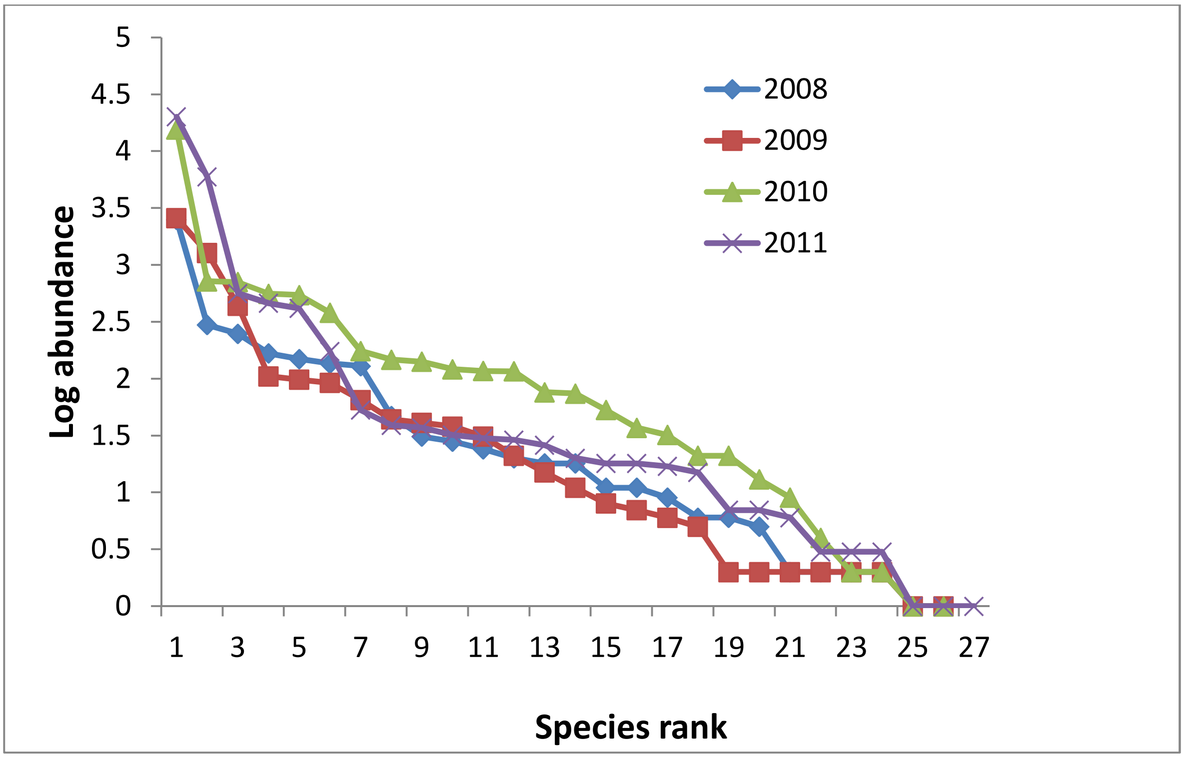


Fig. 10: Rank abundance curve for springtails in Jonkershoek Nature Reserve.

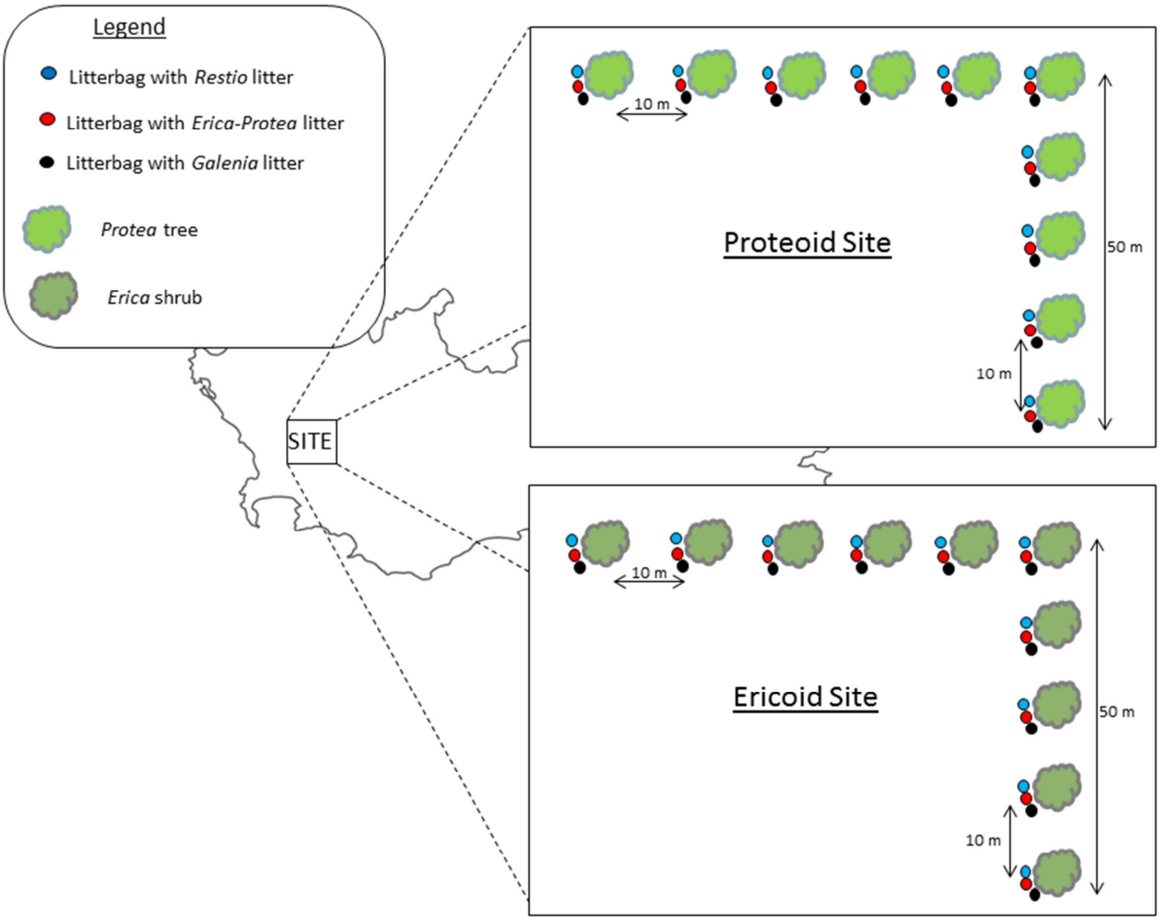


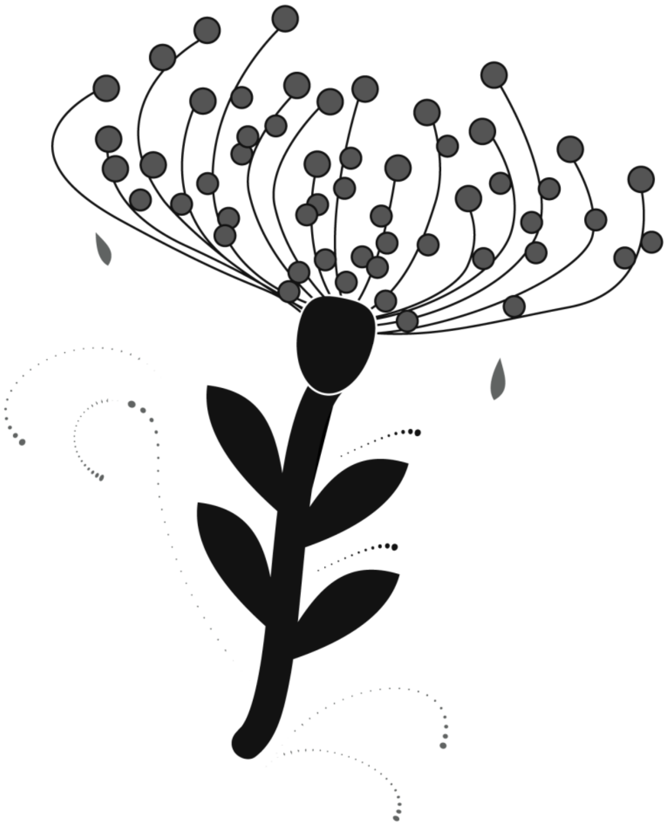
Fig. 11: An illustration of the study design.

Chapter 7

Alpha, beta & gamma diversity

of litter-dwelling Collembola

in the Fynbos biome



Introduction

Despite a strong relationship between large-scale environmental variation and species richness at global scales, some areas clearly stand out as unusually rich. One of the most significant of these is the Fynbos biome at the south-western tip of Africa (Cowling et al. 1992, Mittermeier et al. 2004, Thuiller et al. 2007, Kreft & Jetz 2007). Much attention has been given to documenting the region’s exceptional botanical diversity and understanding the mechanisms underlying it (Goldblatt 1978, Cowling et al. 1996, Linder 2003, Barraclough 2006, Hawkins 2006). While regional plant diversity is indeed high, local diversity is not exceptional compared with similar habitats elsewhere (Cowling et al. 1998). Rather, the high regional diversity has much to do with considerable turnover among local sites (Cowling et al. 1992, Cowling et al. 1996). Indeed, both spatial and temporal beta diversity is high in the biome (Buerki et al. 2012). A diversity of mechanisms is thought to underlie this variation, including limitations to gene flow (landscape barriers, pollinator and phenological specialisations) as well as a highly variable geography and climate resulting in the extreme radiation of the Cape flora (Linder 1991, Linder 2003, Dupont et al. 2011).

If mechanisms such as landscape variation and gene flow limitation are responsible for the patterns in botanical diversity, they may be expected to be present in other groups of organisms, which should then show similarly high regional diversity. Surprisingly few attempts have been made to understand the relationships between local richness, turnover and regional richness of other groups of organisms in the biome. To some extent this may be explained by assessments that vertebrate richness is relatively low here by comparison with other areas (e.g. Chown et al. 2003, Mokhatla et al. 2012). However, for other groups the situation is more complicated. In insects, it was long held that the fynbos is also low in diversity generally (Johnson 1992, Giliomee 2003), though often without a careful distinction between local and regional richness. Yet, it has been shown for endophagous insects that fynbos local diversity is high (Wright & Samways 2000). More recent work has suggested that for phytophagous species local richness may well be high and that regional richness is not lower than other biomes in southern Africa (Procheş & Cowling 2006). For non-phytophagous species, a single study has suggested that local richness is in keeping with what might be expected from available energy (Braschler et al. 2012). One investigation has dealt with turnover, concluding that monkey beetles (Scarabaeidae: Hopliini) show a high turnover in regional richness, which may be linked to the high turnover of plants in the succulent Karoo (Colville et al. 2002). However, because of the close association between these species and their hosts, it appears that the patterns are driven by host species turnover patterns, making any independent assessment of mechanisms problematic. Thus, at present it is not entirely clear what the relationships are between alpha, beta and gamma diversity in the region for most groups, and whether mechanisms that have resulted in current patterns among the plants are operating in other groups.

This situation is especially concerning given on-going modification of habitats by agriculture, urbanization and invasive species, and threats posed by climate change (Rouget et al. 2003). If local beta-diversity is indeed high in many groups, then the removal or degradation of local habitat patches will be as much a threat to other groups as it is to the flora. Here, I therefore investigate local richness, turnover and regional richness of the litter-dwelling springtails of the fynbos biome. This group is not directly associated with plants, making it ideal for an independent examination of diversity patterns, and its members are abundant in the region (Janion et al. 2011a,b, 2012, Liu et al. 2012), likely contributing significantly to soil ecosystem functioning (Janion et al. 2011a).

In this study, I use litterbags to capture the diversity of Collembola in several fynbos sites. In addition, I show that different litter types have an effect on springtail abundance and richness. In particular, I test if species richness or species turnover is important in explaining the richness patterns found. In addition, I compare Collembola richness for the CFR to values found for sites elsewhere across the globe.

Methods and materials

Study sites and experimental technique

Litterbags have been widely used in studies investigating the effect of soil arthropods on the decomposition process, and this method has recently been reviewed by Kampichler & Bruckner (2009). Whilst pitfall traps may give an indication of the surface dwelling species, litterbags can also be used to collect soil species. As a sampling method it is highly comparable to other sampling and extraction techniques such as litter sampling and Tullgren-Berlese extraction (Liu et al. 2012). The litterbags comprise individually numbered cylindrical plastic containers (number of traps and where they were deployed are discussed below) with a height of 4 cm and a diameter of 7.5 cm. The bottom consists of a steel net with mesh size 0.5 mm. The litterbags have a removable lid with 1.6 mm mesh size to allow animals to enter the litterbags, which includes all sizes of Collembola.

Local diversity (alpha)

Previous studies have shown that Collembola may be influenced by different litter types (Hopkin 1997). Litter types were chosen to represent the majority of the fynbos biome and to be comparable to previous studies (Bengtsson et al. 2011, 2012). In Jonkershoek Nature Reserve, three sites, each consisting of different plant communities, was chosen, namely Restioid, Ericoid and Proteoid fynbos. These sites were at least 200 metres apart. In each site, the dominant plant species (i.e. Restioid, Ericacoid or Proteoid) was chosen to ensure that they are interspersed over the whole study site. Five litterbags, each containing a different litter type, were planted under 10 trees/bushes per site during March (thus a total of 50 litterbags per site). The plants were at 10 metres apart. The litter types were *Erica*, *Protea*, *Galenia*, Restio, and *Erica-Protea* mixture. Litterbags were deployed under the bushes within 3-4 cm from another, less than 40 cm from the bush base, on the south-west to south-east side to minimise sun exposure. They were placed in the soil with the top of the litterbags at ground level which allows animals to enter from the top. The total number of litterbags for the experiment in Jonkershoek was 150.

The plants species used for the litter were: 1) *Erica multumbellifera*, collected at Heuningbos (Kleinmond); 2) a *Protea* hybrid (P. *susannae* var '*silva*' and '*cardinal*') collected from Flower Valley, Gansbaai; 3) *Restio multiflorus* collected at White Water Lodge, Stanford; 4) *Galenia africana* (Aizoaceae) collected from an overgrazed rangeland west of the Paarl Mountain, where it is the dominant shrub in the vegetation. It is an indicator of disturbance such as overgrazing and its decomposition rate has been well recorded (Alsopp 1999; Todd & Hoffmann 1999). Although this species is not a common fynbos species, it was included to investigate the effect of a nutrient rich litter type compared to the other nutrient poor ones (see Bengtsson et al. 2011, 2012).

Litter was prepared by collecting plant material of the chosen plant species in the field where they occur in high numbers at the end of the dry season, by cutting the outer 10-20 cm of branches of healthy shrubs. The material was taken to the laboratory, dried at 40° C for at least 24 hours and then stored in open containers at room temperature. The dried plant material was cut into approximately 1 cm long pieces. To estimate initial nutrient content, dry mass and ash-free dry mass, six randomly selected samples of each species were taken when the litter bags are being filled. In the laboratory, the litterbags were filled with air-dried litter up to approx. 3.5 cm, which were weighed to nearest 0.1mg on an electronic balance (FA304T, Avery Berkel, Fairmont, USA). The litter was not compressed but allowed to maintain its normal volume and density. The filled litterbags were stored dry at room temperature before being deployed in the field.

Beta diversity

To assess the diversity and distribution of Collembola in the fynbos biome, Collembola were sampled in several protected areas across the Western Cape. The sites included were Jonkershoek Nature Reserve, Kogelberg Biosphere Reserve, Mont Rochelle (Franschoek) Nature Reserve, Table Mountain National Park (Peninsula Section), Wilderness National Park (Rondevlei section) and Bontebok National Park (Fig. 1A, B, Supplementary material Table 1). In these sites, Collembola were sampled using litterbags with only two different litter types, *Galenia africana*, and an *Erica-Protea* litter mixture.

At each site two sites were chosen at least 200 metres apart (Ericoid and Proteoid). Two litterbags each containing a different littertype (*Protea-Erica* mixture and *Galenia*) were deployed under the dominant plant species in the respective sites at the end of summer (March/April), left undisturbed and subsequently collected in September (2008) or in July or August (2009-2011). Litterbags were deployed in an L-shape transect (estimated sample unit coverage of 2500 m^2) to cover a wider area of each of the proteoid and ericoid sites (Supplementary material Fig. 7). Each tree or shrub underneath which litterbags were deployed was approximately 10 metres apart. The litterbags were deployed under the trees or shrubs within 3-4 cm from another, less than 40 cm from the bush base, on the south-west to south-east side to minimise sun exposure. They were placed in the soil with the top of the litterbags at ground level which allows invertebrates to enter from the top. Thus, the total number of litterbags at each site was 40, 10 *Galenia* and 10 *Erica-Protea* mixtures in each site. The litterbags were deployed in March/April, left undisturbed and collected after three months during the rainy season when Collembola abundance are known to be high (July or August) (Liu et al. 2012). Three months were chosen because the decomposition rate is already known for *Galenia africana* (half-life = 100 days), and if left longer than four months almost no litter will remain in the litterbag (Bengtsson et al. 2011, 2012). Upon collection the litterbags were taken out of the soil, wrapped in aluminium foil to prevent any animals from escaping and immediately placed individually in plastic bags and stored upright in a cool, thermally insulated container and returned to the laboratory within five hours of collection.

For extraction of animals, litterbags were inverted in a custom-built high-gradient extractor (Central Mechanical Services, Stellenbosch University), with heating from above (see Macfadyen 1953, Block 1966) and cooling from below by means of a temperature controlled water bath (Grant R2, Cambridge, UK). The extraction into 100% propylene glycol took approximately four days. After extraction the animals were transferred to 99.9% ethanol for identification and barcoding (see below). The dry litter samples in each litterbag were transferred to aluminium foil and dried at 50° for at least 24 hours to ensure that the samples are dry before storage. Little organic material was lost during the extraction process.

Species identification

Morphospecies were identified using important morphological characters and European keys available to determine the family or possibly the genus level (Fjellberg 1998, 2007, Bretfield 1999, Potapov 2001, Hopkin 2007). As the springtail fauna of South Africa is not well understood (Janion et al. 2011a, Chapter 2), I used morphospecies to compare species between sites. In several cases however, species identification could be verified, mostly for well-known European species (introduced species). Irrespective, the morphospecies approach is widely used and the level of systematic knowledge for the group for the region developed by the broader project (see Janion et al. 2011a) is sufficient to provide confidence that morphospecies are representative of the biological situation (i.e. species level differences are being assessed, rather than genus level or some other arbitrary criterion).

Statistical analyses

Local diversity (alpha)

Sampled-based rarefaction curves were plotted to examine the degree of sampling efficiency and to determine the predicted number of species in the site, using EstimateS V8.2.0 (Colwell 2009). Rarefaction methods allow for standardization of data to make meaningful comparisons between datasets (Gotelli & Colwell 2001). As sample-based rarefaction curves use species density (number of species per unit area), individual-based rarefaction curves were estimated using EstimateS V8.2.0 (Colwell 2009), as these compare species richness values of sites. Sampling is considered adequate when the rarefaction curves and the estimators converge at the highest observed values (Longino et al. 2002). Species accumulation curves were plotted using PRIMER V6.0 (Clarke & Warwick 2001). In addition, rank abundance curves were plotted for each site to evaluate which species were most abundant.

To examine the effect of litter type in local species richness, the differences in springtail species richness and abundance between the five different litter types and three different sites in Jonkershoek Nature Reserve were examined using a generalized linear model. A quasi-Poisson model was used as the data were overdispersed, and all analyses were done without log transformation, as recent studies showed that count data performed better when data is not transformed (O'Hara & Kotze 2010). The effect of species richness and abundance on decomposition rate was also examined using a generalized linear model with a Quasi-poisson distribution. For the calculation of decomposition rates see Bengtsson et al. (2011, 2012). Any interactions found not to be significant was removed (after Crawley 2007). All analyses were undertaken in R version 2.15.1.

Beta diversity

Turnover (beta diversity) between sites was calculated using a method recently proposed by Carvalho et al. (2012), which distinguishes between the contribution of species replacement and species richness. First the B_{cc} complementary measure was calculated (Colwell & Coddington 1994), also known as the Jaccard dissimilarity measure:

$$Bcc = \frac{b+c}{a+b+c}$$

where *a* is the number of species common to both sites (in this case years), *b* is the number of species exclusive to the first site, and *c* is the number of species exclusive to the second site.

Replacement is calculated as the substitution of *n* species in one site from *n* species in another site (Carvalho et al. 2012).

$$B_{-3} = \frac{2 \times \min(b, c)}{a + b + c}$$

B_{rich} is the absolute difference in species richness between sites is calculated by:

$$B_{rich} = \frac{|b - c|}{a + b + c}$$

Thus, according to Carvalho et al. (2012) beta diversity (B_{cc}) consists of two components, replacement (B_{-3}) and species richness (B_{rich}) differences:

$$B_{cc} = B_{-3} + B_{rich}$$

To compare species richness and abundance between sites, a generalized linear model assuming a quasi-Poisson distribution was use (R version 2.15.1).

Differences in springtail assemblages between sites were compared using multivariate analyses in PRIMER V6.0 (Clarke & Warwick 2001). Abundance data were square root transformed to down-weight common species, and a Bray-Curtis similarity index was used to calculate similarity between assemblages. A one-way Analysis of Similarity (ANOSIM) was undertaken with all the sites combined. Here a *Global R* value is obtained, with a value closer to 1 indicating more dissimilarity. Similarly for each site and all sites combined respectively, the difference in assemblages was plotted using non-metric multi-dimensional scaling (nMDS). If the stress value obtained is smaller than 0.2, then the representation is assumed to be valid.

To compare the results to other studies, I collected literature recording springtail species richness. The following information was collected: the number of species recorded in the sampling site, the coordinates of the sampling site (if not given we collected the latitude and longitude to the area as close as possible) and the vegetation sampled in. It has been shown that together with area and winter length, temperature is a main predictor of springtail species richness in Europe (Ulrich & Fiera 2009). Thus, I examined the relationship between temperature and springtail species richness by using data obtained from WorldClim (Hijmans et al. 2005). In addition, as springtails are vulnerable to desiccation (Hopkin 1997), I also investigated the relationship between species richness and precipitation. Mean temperature values were obtained from the dataset MODIS/Terra Land Surface Temperature/Emissivity Monthly L3 Global 0.05Deg CMG (Hijmans *et al.* 2005). An average of day and night temperatures were used obtain mean temperatures. Mean annual precipitation was also derived from the WorldClim (Hijmans *et al.* 2005).

Results

A total of 17,408 individuals and 114 morphospecies from 14 families were found in the six sites (Table 1, 2). Table 1 indicates the total number of species found per site, as well as the estimated species richness for Jacknife2 and Chao 1. The species richness estimators were higher in all cases. The species accumulation curves did not reach an asymptote in a few cases, such as Mont Rochelle, Bontebok and Kogelberg (Supplementary material, Figs 1A-6A). Peninsula had the highest abundance of all sites (6731 individuals) while Bontebok had the lowest abundance (295 individuals). In terms of species richness, Kogelberg had the highest number of species (32 species), while Bontebok had the lowest (14 species). This low value for species richness and abundance for Bontebok may be an artefact of the high level of disturbance. This National Park is intensively managed with fire to increase grazing for bontebok with the fire intervals have decreased over the last few decades (Kraaij 2010), thus this may have had an influence on the springtail diversity and abundance we found.

Rank abundance curves are shown for each site (Supplementary material, Figs 1B-6B). *Ceratophysella* cf. *denticulata* was the dominant species in the Kogelberg and Peninsula sites (Supplementary material, Fig. 2B, 4B). Although these sites are in natural areas, they are visited frequently by humans and were in the vicinity of hiking paths. This potentially introduced species is usually common in disturbed sites. In contrast, the endemic *Parisotoma* species were dominant in Mont Rochelle and Jonkershoek (Supplementary material, Fig. 1B, 5B), while the endemic *Austrogastura* was dominant in Wilderness (Supplementary material, Fig. 6B).

When investigating the effects of litter type and site on springtail species richness and abundance in Jonkershoek Nature Reserve using five litter types, litter types *Galenia*, *Protea* and *Restio* influenced species richness (Fig. 2A, Table 3A), while litter types *Erica-Protea* mixture, *Galenia* and *Protea* significantly influenced abundance (Fig. 2B, Table 3B). Here site did not affect species richness, although the *Restio* site had an effect on abundance (Table 3B). The *Erica* and *Protea* litter in the *Erica* site had high numbers of springtails compared to the other litter types and sites (Fig. 2B). When comparing species richness and abundance between nature reserves, sites (except Bontebok) was found to have a significant effect on species richness and abundance, while *Galenia* litter was also found to be significant for species richness (Table 4A, B). Interestingly, the interaction between *Galenia* litter and all sites (except Bontebok) was found to be significant for species richness (Table 4B).

Assemblages differed significantly between sites, which is illustrated in the nMDS plot (Fig. 3). From the calculation of beta diversity (B_{cc}), it is clear that turnover is due to change in species replacement, and not species richness (Figs. 4A, Supplementary material, Table 2). This is reflected in the dendrograms of B_{cc}, B_{rich} and B_{-3} (Fig. 4A-C), and the resemblance matrix of B_{rich} and B_{-3} (Supplementary material, Table 2). The Jonkershoek, Kogelberg and Peninsula sites are most similar, while the Bontebok site differs from all other sites.

A summary of the literature used to compare with this study is shown in Supplementary material (Table 3). When comparing the results from this study to others worldwide, it seems that for at least for temperature and precipitation for Kogelberg, the species richness patterns seem to be similar to another Mediterranean-type system in Spain (Fig. 5, 6).

Discussion

Documenting and explaining the relative diversity of the Cape Floristic Region (CFR), measured as species richness, has long been a focus of ecology (Cowling et al. 1992, 1996, Goldblatt & Manning 2002, Thuiller et al. 2007). The exceptionally high plant diversity has been widely discussed (most recently by e.g. Kreft & Jetz 2007) and some factors thought to drive these include a highly variable climate and geography (Linder 2003). In fact, the CFR is one of the hotpots of biodiversity (Myers et al. 2000, Mittermeier et al. 2004). Earlier studies suggest that insect species richness is low in the CFR when compared to the high plant richness (Giliomee 2003). However, more recent studies have shown otherwise. Wright &

Samways (1998) found that gall-insect species richness was positively correlated with the Cape Floristic Region (CFR) plant species richness. Using more groups of insects, this relationship was also found by Procheş & Cowling (2006) and Procheş et al. (2009). It has been suggested that local richness is in keeping with what might be expected from available energy (Braschler et al. 2012). Similar observations have been found for ants and beetles (Botes et al. 2006, 2007). This also seems to be the case for springtails. By comparison with species richness data from a range of regions, species richness found in this study was not unexpected. It seems to be slightly lower when compared to other similar areas in terms of the temperature-richness relationship, while being more similar to values from other areas in terms of expectations based on a precipitation-richness relationship. Ulrich & Fiera (2009) showed for the Northern Hemisphere, that area, winter length and temperature are important predictors of springtail species richness. However, due to undersampling especially in the Southern Hemisphere, these comparisons are not easy to generalize. Nonetheless, the study undertaken here certainly suggests that the generalizations are more broadly applicable. Given changes in taxonomic approaches and the advent of modern techniques such as DNA barcoding, more countries being sampled intensively (e.g. Abrantes et al. 2010), and future data should make generalization more feasible. Be that as it may, this work bears out, for the springtails, the idea that the Fynbos biome is not woefully poor in arthropod richness, as was originally thought (Marloth 1908, Johnson 1992). Rather, richness is in keeping with what might be expected for similar systems globally given energy availability (for a comprehensive recent discussion see Brachler et al. 2012). Of course, for host-specific species, other patterns may well be found.

The spatial variation in diversity has been at the heart of explanations for the high richness of plant species in the Fynbos biome. In particular, local (alpha) diversity tends to be low, but beta diversity high, resulting in considerable regional diversity (Cowling et al. 1992). Although Procheş et al. (2009) predicted high beta diversity of insect groups to explain high regional insect diversity, this has not been well investigated for insects, or indeed for any other invertebrates. Invertebrate species richness and abundance was significantly influenced by fynbos type and elevation on Table Mountain (Pryke & Samways 2008). In the same study, species richness was higher in the fynbos than in the forest, although this was not found to be as a result of beta diversity. However, in the succulent Karoo high beta diversity was found for monkey beetles (Scarabaeidae: Hopliini) which was thought to closely match plant beta diversity (Colville et al. 2002). In this study, high beta diversity of springtails was largely to do with species replacement, as indicated by the contribution of the two measures, B_{rich} and B_{-3} (Figs. 4A-C). Thus, there is considerable evidence that turnover is playing a significant role by comparison with changes in species richness. This is to some extent similar as observed for plants in the CFR (Thuiller et al. 2007). Nonetheless, some nuances are present. Thus, at the local scale (within *Protea* and *Erica* sites) alpha diversity was found to be low. By contrast, at the regional (among national park) scale, beta is high. Thus, unlike the fynbos plants, it is regional beta diversity that contributes most to the variation in regional richness. Thus, whatever mechanisms are driving high local beta-diversity in the plants, they may well be specific to that group, rather than more general. In consequence, the current study may help narrow down the considerable number of mechanisms proposed to account for plant diversity in the region (Linder 2003). In particular, it suggests that evolutionary mechanisms, rather than current ecological ones, deserve further attention.

Several sites in this study had unique springtail species, suggesting a high level of endemism. Most species shared between sites were potentially introduced species or species with a widespread distribution, while more than 70% of the species were endemic to most sites (Table 2). Indeed, an important aspect of fynbos plants is the high levels of local and regional endemism, which is amongst the highest in the world (Cowling & Holmes 1992, Cowling et al. 1992). For insects, the Table Mountain and Peninsula area is a hotspot for endemic insect species (Picker & Samways 1996, Pryke & Samways 2008, 2010). Studies have also found the Cape Floristic Region to be the hotspot of endemism for insect species such as dragonflies (Picker & Samways 1996) and gall-insects (Wright & Samways 1998). The conservation of these biodiversity hotspots is therefore essential as they may comprise of many localised endemics and undiscovered species.

High local diversity was found for springtails, which was affected by litter type. Although local springtail species richness was not affected by litter type or site, the abundance differed between litter type and site. In particular, at Jonkershoek, the *Erica* and *Protea* litter types in the *Erica* site had high abundances of Collembola, while the *Galenia* litter had the lowest. This is contrary to the expectation that the litter with the highest nutrient content would have the highest number of springtails. Decomposition rate was found to be highest for *Galenia* (mass loss of 0.6904 g), while lower for the *Erica* and *Protea* litter (mass loss 0.2420 and 0.35 g respectively, measured as the proportion of litter remaining after a certain period, Bengtsson et al. 2012). Thus, one explanation might be that due to higher mass loss of *Galenia* litter, there was no suitable habitat left for springtails by the end of the winter. Conversely, the *Erica* and *Protea* litter types, which have a lower decomposition rate and thus more litter left during the sampling period (Bengtsson et al. 2012) might have been more suitable for springtails. In this study, a positive relationship was found between decomposition rate and Collembola species richness.

In plantations, higher Collembola abundances have been associated with the decompositional properties of the environment, including higher moisture content and C:N ratios of leaf-litter and soil (Robson et al. 2009). Similarly, Liu et al. (2012) found a positive relationship between site humidity and Collembola richness and abundance. Vegetation can have an impact on the diversity of soil biota by means of litter production affecting the soil system (Wardle 2002). This has been shown experimentally, where mite species richness and abundance showed an increase in mixed-species litter bags compared with single-species litter bags (Kaneko & Salamanca 1999). However, it has been suggested that litter quality is more important than litter quantity (Salamon et al. 2004). In another study, it was suggested than an increase in plant diversity cause an increase in resources available to Collembola, ultimately causing an increase in diversity and density of Collembola (Sabais et al. 2011). This may also be possible in the fynbos, although more comparative studies are necessary before any generalisations can be made.

The dominance of a potentially introduced species, *Ceratophysella* cf. *denticulata*, is especially concerning given the potential impact invasive springtails can have on local fauna (Terauds et al. 2011). In fact, it was found that an invasive springtail, *Hypogastrura manubrialis*, is dominant in remnant patches of renosterveld (Leinaas et al. in prep., although this area was in a disturbed landscape). Further work is underway to understand the interactions between invasive and endemic springtails, and more controlled experiments will be needed to disentangle the effects of different species, litter types and their interactions. Understanding the diversity patterns of soil animals is important to understand how they will respond to global change, and in turn affect the delivery of ecosystem services (Lavelle et al. 2006).

Scope of contribution of the candidate

Writing and analyses was done by the candidate.

References

Abrantes, E.A., Bellini, B.C., Bernardo, A.N., Fernandes, L.H., Mendonca, M.C., Oliveira, E.P., Queiroz, G.C., Sautter, K.D., Silveira, T.C. & Zeppelini, T.C. (2010) Synthesis of Brazilian Collembola: an update to the species list. *Zootaxa* **2388**, 1-22.

Allsopp, N. (1999) Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. *Plant Ecology* **142**, 179-187.

Barraclough, T.G. (2006) What can phylogenetics tell us about speciation in the Cape flora? *Diversity and Distributions* **12**, 21–26.

Bengtsson, J., Janion, C., Chown, S.L. & Leinaas, H.P. (2011) Variation in decomposition rates in the fynbos biome, South Africa: the role of plant species and plant stoichiometry. *Oecologia* **165**, 225-235.

Bengtsson, J., Janion, C., Chown, S.L. & Leinaas, H.P. (2012) Litter decomposition in the fynbos vegetation, South Africa. *Soil Biology & Biochemistry* **47**, 100-105.

Block, W. (1966) Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods. *Oikos* **17**, 1-9.

Botes, A., McGeoch, M.A. & Chown, S.L. (2007) Ground-dwelling beetle assemblages in the northern Cape Floristic Region: patterns, correlates and implications. *Austral Ecology* **32**, 210-224.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P. & Chown, S.L. (2006) Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**, 71-90.

Braschler, B., Gaston, K.J. & Chown, S.L. (2012) The Fynbos and Succulent Karoo biomes do not have exceptional local ant richness. *PloSONE* **7**, e31463.

Bretfield, G. (1999) *Synopses on Palaearctic Collembola, Volume 2, Symphypleona*. W. Dunger (Ed). Staatliches Museum für Naturkunde, Görlitz.

Buerki, S., Jose S, Yadav, S.R., Goldblatt, P., Manning, J.C. & Forest, F. (2012) Contrasting biogeographic and diversification patterns in two Meditteranean-type ecosystems. *Plos One* **7**, e39377.

Carvalho, J.C., Cardoso, P. & Gomes, P. (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography* **21**, 760-771.

Cassagne, N., Gauquelin, T., Bal-Serin, M-C. & Gers, C. (2006). Endemic Collembola, privileged bioindicators of forest management. *Pedobiologia* **50**, 127-134.

Chauvat, M., Trap, J., Perez, G., Delporte, P. & Aubert, M. (2011) Assemblages of Collembola across a 130-year chronosequence of beech forest. *Soil Organisms* **83**, 405-418.

Chown, S.L., van Rensburg, B.J., Gaston K.J., Rodrigues, A.S.L. & van Jaarsveld A.S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* **13,** 1233–1241.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edition. Plymouth Marine Laboratory, UK: PRIMER-E Ltd.

Colville, J. Picker, M.D. & Cowling R.M. (2002) Species turnover of monkey beetles (Scarabaeidae: Hopliini) along environmental and disturbance gradients in the Namaqualand region of the succulent Karoo, South Africa. *Biodiversity & Conservation* **11**, 243-264.

Colwell, R.K. (2009) EstimateS – statistical estimation of species richness and shared species from samples. V8.20. http://viceroy.eeb.uconn.edu/EstimateSPages/EstimateS.flx.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical transactions of the Royal Society of London B* **345**, 101-118.

Cowling, R.M. & Holmes, P.M. (1992) Endemism and speciation in a lowland flora from the Cape Floristic Region. *Biological Journal of the Linnean Society* **47**, 367-383.

Cowling, R.M., Holmes, P.M. & Rebelo, A.G. (1992) Plant diversity and endemism. In: *The Ecology of Fynbos: Nutrients, Fire and Diversity* (ed. by R.M. Cowling). Oxford University Press, Cape Town, pp. 62-112.

Cowling, R.M., MacDonald, I.A.W. & Simmons, M.T. (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. Biodiversity and Conservation 5, 527-550.

Cowling, R.M., Rundel, P.W., Desmet, P.G. & Esler, K.J. (1998) Extraordinary high regional-scale plant diversity in southern African arid lands: subcontinental and global comparisons. *Diversity and Distributions* **4**, 27-36.

Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd, Chichester.

Culik, M.P., de Souza, J.L. & Ventura, J.A. (2002) Biodiversity of Collembola in tropical agricultural environments of Espírito Santo, Brazil. *Applied Soil Ecology* **21**, 49-58.

Dupont, L.M., Linder, H.P., Rommerskirchen, F. & Enno Schefuß, E. (2011) Climate-driven rampant speciation of the Cape flora. *Journal of Biogeography* **38**, 1059–1068.

Fjellberg, A. (1998) *Fauna Entomologica Scandinavica Volume 35. The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha*. Brill, Leiden.

Fjellberg, A. (2007) *Fauna Entomologica Scandinavica Volume 42. The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona*. Brill, Leiden.

Giliomee, J.H. (2003) Insect diversity in the Cape Floristic Region. *African Journal of Ecology* **41**, 237-244.

Gotelli, J.N. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**, 379 - 391.

Greenslade, P. & Smith, D. (1999) The epigaeic arthropod fauna of Buttongrass moorland in Tasmanian Wilderness World Heritage Area. In: *The Other 99%. The Conservation and Biodiversity of Invertebrates*. W. Ponder & D. Lunney (Eds), pp. 90-94, Transactions of the Royal Society of New South Wales, Mosman.

Goldblatt, P. (1978) An analysis of the flora of Southern Africa: its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden* **65**, 369-436.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape region of Southern Africa. *Annals of the Missouri Botanical Garden* **89**, 281–302.

Hawkins, J.A. (2006) Using phylogeny to investigate the origins of the Cape flora: the importance of taxonomic, gene and genome sampling strategies. *Diversity and Distribution* **12**, 27–33.

Hijmans, R.J., Cameron, S.E. , Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25,** 1965-1978.

Hopkin, S. (1997) *Biology of the Springtails. Insecta: Collembola*. Oxford University Press, Oxford.

Hopkin, S. (2007) *A Key to the Collembola (Springtails) of Britain and Ireland*. FSC, London.

Janion, C., Bedos, A, Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, Liu, A., Malmström, A., Porco, D., and Chown, S.L. (2011a) Springtails diversity in South Africa. *South African Journal of Science* **107**, Article #582, 7 pages.

Janion, C, Bedos, A., Deharveng, L. (2011b) The genus *Ectonura*, Cassagnau 1980 in South Africa (Collembola: Neanuridae: Neanurinae), with a key to South African Neanurinae. *ZooKeys* **136**, 31-45.

Janion, C., D'Haese, C. and Deharveng, L. (2012) A new species and first record of the genus *Triacanthella* Schaffer, 1897 (Collembola, Hypogastruridae) for Africa. *Zookeys* **163**, 57-68.

Johnson, S.D. (1992) Plant–animal relationships. In: *The Ecology of Fynbos: Nutrients, Fire and Diversity* (ed. by R.M. Cowling). Oxford University Press, Cape Town, pp. 175–205.

Kampichler, C. & Bruckner, A. (2009) The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews* **84**, 375-389.

Kaneko, N. & Salamanca, E.F. (1999) Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecological Research* **14**, 231-138.

Kraaij, T. (2010) Changing the fire management regime in the renosterveld and lowland fynbos of the Bontebok National Park. *South African Journal of Botany* ***76***, 550-557.

Kreft, H. & Jetz, W. (2007) Global Patterns and Determinants of Vascular Plant Diversity. *Proceedings of the National Academy of Sciences of the Unites States of America* **104**, 5925–5930.

Linder, H.P. (1991) Environmental correlates of patterns of species richness in the south-western Cape Province of South Africa. *Journal of Biogeography* 18, 509-518.

Linder, H.P. (2003) The radiation of the Cape flora, southern Africa. *Biological Reviews* **78**, 597-638.

Liu, A., Janion, C. & Chown, S.L. (2012) Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations. *Pedobiologia* **55**, 203-209.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology* **83**, 689-702.

Macfadyen, A. (1953) Notes on methods for the extraction of small soil arthropods. *Journal of Animal Ecology* **22**, 65-77.

Marloth, R. (1908) Some observations on entomophilous flowers. *South African Journal of Science* **4**, 110-113.

Mittermeier, R.A., Robles-Gil, P., Hoffmann, M., Pilgrim, J.D., Brooks, T.M., Mittermeier, C.G., Lamoreux, J.L., Fonseca, G. (2004) *Hotspots Revisited: Earth's Biologically Richest and Most Threatened Terrestrial Ecoregions*. Cemex & Conservation International, Mexico City.

Mokhatla, M.M., Measey, G.J., Chimimba, C.T. & van Rensburg, B.J. (2012) A biogeographical assessment of anthropogenic threats to areas where different frog breeding groups occur in South Africa: implications for anuran conservation. *Diversity and Distributions* **18**, 470-480.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 583-858.

O'Hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution* **1**, 118-122.

Petersen, H. (2011) Collembolan communities in shrublands along climatic gradients in Europe and the effect of experimental warming and drought on population density, biomass and diversity. *Soil Organisms* **83**, 463-488.

Picker, M.D & Samways, M.J. (1996) Faunal diversity and endemicity of the Cape Peninsula, South Africa- a first assessment. *Biodiversity and Conservation* **5**, 591-606.

Potapov, M. (2001) *Synopses on Palaearctic Collembola, Volume 3, Isotomidae*. W. Dunger, W. (Ed). Staatliches Museum für Naturkunde, Görlitz.

Procheş, S. & Cowling, R.M. (2006) Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecology and Biogeography* **15**, 445-451.

Procheş, S., Forest, F., Veldtman, R, Chown, S.L., Cowling, R.M., Johnson, S.D., Richardson, D.M. & Savolainen, V. (2009) Dissecting the plant-insect diversity relationship in the Cape. *Molecular Phylogenetics and Evolution* **51**, 94-99.

Pryke, J.S. & Samways, M.J. (2008) Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation* **17**, 3027-3043.

Pryke, J.S. & Samways, M.J. (2010) Significant variables for the conservation of mountain invertebrates. *Journal of Insect Conservation* **14**, 247-256.

Querner, P. & Bruckner, A. (2010) Combining pitfall traps and soil samples to collect Collembola for site scale biodiversity assessment. *Applied Soil Ecology* **45**, 293-297.

Robson, T.C., Baker, A.C. & Murrray, B.R. (2009) Differences in leaf-litter invertebrate assemblages between radiata pine plantations and neighbouring native eucalypt woodland. *Austral Ecology* **34**, 368-376.

Rochefort, S., Therrien, F., Shetlar, D.J. & Brodeur, J. (2006) Species diversity and seasonal abundance of Collembola in turfgrass ecosystems of North America. *Pedobiologia* **50,** 61-68.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* **112**, 63-85.

Sabais, A.W.C., Scheu, S. & Eisenhauer, N. (2011) Plant species richness drives the density and diversity of Collembola in temperate grassland. *Acta Oecologia* **37**, 195-202.

Salamon, J.-A., Schaefer, M., Alphei, J., Schmid, B. & Scheu, S. (2004) Effects of plant diversity on Collembola in an experimental grassland ecosystem. *Oikos* **106**, 51-60.

Salmon, S., Bedos, A., Villemant, C., Rome, Q., Daugeron, C. & Deharveng, L. (2010) Diversity, structure and endemicity of earthworm and springtail communities of a softly managed beech forest in the Pyrenees (France). *Rev. Ecol. (Terre Vie)* **65**, 45-62.

Terauds, A., Chown, S.L. & Bergstrom, D.M. (2011) Spatial scale and species identity influence the indigenous –alien relationship in springtails. *Ecology* **92**, 1436-1447.

Thuiller, W., Slingsby, J.A., Privett, S.D.J. & Cowling, R.M. (2007) Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. *PLoS ONE* **9**, e938.

Todd S.W. & Hoffmann, M.T. (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology* **142**, 169-178.

Ulrich, W. & Fiera, C. (2009) Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologia* **35**, 45-52.

Uvarov, A.V. & Byzova, J.B. (1995) Species diversity and distribution of Collembola in the vicinity of Polish Polar Station, Hornsund area, Spitsbergen. *Polish Polar Research* **16**, 233-243.

Wardle, D.A. (2002) *Communities and Ecosystems. Linking the aboveground and belowground components*. Princeton University Press, Princeton.

Wright, M. & Samways, M.J. (1998) Insect species richness tracking plant species richness in a diverse flora: gall insects in the Cape Floristic Region, South Africa. *Oecologia* **115**, 427-433.

Wright, M.G. & Samways, M.J. (2000) Biogeography and species richness of endophagous insects associated with Proteaceae in South Africa. *African Journal of Ecology* **38**, 16-22.

Zeppelini, D., Bellini, B.C., Creão-Duarte, J. & Hernández, M.I.M. (2009) Collembola as indicators of restoration in mined sand dunes of Northeastern Brazil (2009) Biodiversity and Conservation **18**, 1161-1170.

Tables

Table 1: Summary of total species richness, abundance, and estimated species richness ± SD per site (n=40).

TOTAL	**Peninsula**	**Jonkershoek**	**Kogelberg**	**Mont Rochelle**	**Bontebok**	**Wilderness**
Total abundance	6731	2948	2581	2281	295	2572
Total species richness	26	20	32	27	14	25
Jacknife 2 (with re-sampling)	30.88 ± 2.07	21.7	38.83 ± 3.09	33.83 ± 2.75	18.88 ± 2.07	30.85 ± 2.23
Chao 1	30.17 ± 4.88	20	38.25 ± 7.55	28.5 ± 2.29	18 ± 5.29	26.5 ± 2.29

Table 2: Collembola abundances of springtail species found in the six sites investigated. EP= Erica site, Peninsula, PP=Protea site, Peninsula, EM=Erica site Mont Rochelle, PM=Protea site, Mont Rochelle, EW=Erica site, Wilderness, PW=Protea site, Wilderness, EK=Erica site Kogelberg, PK=Protea site Kogelberg, EJ=Erica site Jonkershoek, PJ=Protea site Jonkershoek, EB=Erica site Bontebok, PB=Protea site Bontebok.

	EP	**PP**	**EM**	**PM**	**EW**	**PW**	**EK**	**PK**	**EJ**	**PJ**	**EB**	**PB**
Order Entomobryomorpha												
Cyphoderidae												
Cyphoderidae sp. 1	7	1	0	0	0	0	0	0	0	0	0	0
Cyphoderidae sp. 2	0	0	0	0	1	0	0	0	0	0	0	0
Entomobryidae												
Entomobryidae sp. 1	0	0	0	0	0	5	0	0	0	0	0	0
Isotomurus sp. 1	2	0	0	0	0	0	1	2	17	0	0	1
Lepidocyrtus sp. 1	0	0	0	0	0	0	93	25	47	66	0	0
Lepidocyrtus sp. 2	0	0	6	162	0	0	0	0	0	0	0	0
Lepidocyrtus sp. 3	171	117	0	0	0	0	0	0	0	0	0	0
Lepidocyrtus sp. 4	0	0	0	0	59	595	0	0	0	0	0	0
Pseudosinella sp. 1	0	0	0	0	0	0	13	6	0	0	0	22
Pseudosinella sp. 2	0	0	0	2	0	0	0	0	0	0	0	0
Pseudosinella sp. 3	1	62	0	0	0	0	0	0	0	0	0	0
Pseudosinella sp. 4	0	0	0	0	0	9	0	0	0	0	0	0
Seira sp. 1	0	0	0	0	0	0	1	0	0	0	0	0
Seira sp. 2	0	0	1	0	0	0	0	0	0	0	0	0
Seira sp. 3	0	0	0	0	1	1	0	0	0	0	0	0
Seira sp. 4	0	0	0	0	0	0	4	3	0	0	0	0
Seira sp. 5	0	0	0	2	0	0	0	0	0	0	0	0
Seira sp. 6	0	0	0	0	0	0	0	0	0	0	22	21
Seira sp. 7	0	0	0	0	48	2	0	0	0	0	0	0
Seira sp. 8	0	0	0	0	0	0	0	0	0	0	6	35
Seira sp. 9	0	0	0	0	0	0	2	9	12	6	0	0
Seira sp. 10	2	1	0	0	0	0	0	0	0	0	0	0
Seira sp. 11	0	0	0	0	0	0	18	3	0	0	0	0
Seira sp. 12	6	6	0	0	0	0	0	0	0	0	0	0
Seira sp. 13	7	14	27	1	0	0	9	22	11	6	0	0
Seira sp. 14	0	0	0	0	6	10	0	0	0	0	0	0
Seira sp. 15	0	0	9	4	0	0	0	0	0	0	0	0
Seira sp. 16	0	0	0	0	2	22	0	0	0	0	0	0
Seira sp. 17	0	0	0	0	0	0	0	0	1	2	0	0
Isotomidae												
Cryptopygus sp. 1	0	0	0	0	0	0	0	0	73	3	0	0
Cryptopygus sp. 2	2	0	0	0	0	0	0	0	0	0	0	0
Cryptopygus sp. 3	0	0	3	0	0	0	1	1	0	0	0	0

	EP	PP	EM	PM	EW	PW	EK	PK	EJ	PJ	EB	PB
Cryptopygus sp. 4	0	0	0	0	0	0	22	111	0	0	0	0
Cryptopygus sp. 5	0	0	0	0	0	0	0	0	0	0	0	29
Cryptopygus sp. 6	0	0	149	25	0	0	0	0	0	0	0	0
Cryptopygus sp. 7	0	0	0	0	0	0	22	7	0	0	0	0
Cryptopygus cf. caecus	726	43	21	38	2	1	1	23	53	54	0	0
Folsomides cf. parvulus	0	0	0	0	40	41	1	0	0	0	0	0
Hemisotoma sp.	0	0	0	0	9	0	0	0	0	0	0	0
Isotoma sp. 1	0	0	0	0	0	0	0	0	0	0	0	1
Isotoma sp. 2	0	0	3	12	0	0	0	0	0	0	0	0
Isotoma sp. 3	3	1	0	0	0	0	0	0	0	0	0	0
Isotoma sp. 4	0	0	0	0	0	0	316	39	0	0	0	0
Parisotoma sp. 1	0	0	0	0	0	0	0	0	0	0	4	3
Parisotoma sp. 2	0	0	0	0	0	0	258	324	0	0	0	0
Parisotoma sp. 3	0	0	797	255	0	0	0	0	0	0	0	0
Parisotoma sp. 4	1323	412	0	0	0	0	0	0	0	0	0	0
Parisotoma sp. 5	0	0	0	0	0	0	0	0	1503	511	0	0
Parisotoma sp. 5	0	0	0	0	182	292	0	0	0	0	0	0
Proisotoma sp. 6	0	0	8	0	0	0	0	0	0	0	0	0
Proisotoma sp. 7	0	0	0	0	2	0	0	0	0	0	0	0
Order Neelipleona												
Neelidae												
Megalothorax sp.	166	5	0	0	0	0	3	0	0	0	0	0
Order Poduromorpha												
Brachystomellidae												
Brachystomella sp. 1	0	0	0	0	0	0	0	0	45	125	0	0
Brachystomella sp. 2	0	0	0	0	96	2	0	0	0	0	0	0
Brachystomella sp. 3	0	0	0	0	0	0	163	80	0	0	0	0
Brachystomella sp. 4	0	0	10	41	0	0	0	0	0	0	0	0
Brachystomella sp. 5	118	40	0	0	0	0	0	0	0	0	0	0
Hypogastruridae												
Austrogastrura sp. 1	0	0	0	55	0	0	0	0	0	0	0	0
Austrogastrura sp. 2	1	1	0	0	0	0	0	0	0	0	0	0
Austrogastura sp. 3	0	0	0	0	813	32	0	0	0	0	0	0
Ceratophysella cf. denticulata	1122	2120	0	1	0	0	154	537	0	0	0	0
Hypogastruridae sp.	0	0	0	2	0	0	0	0	0	0	0	0
Triacanthella sp. 1	0	0	0	0	0	0	0	0	194	54	0	0
Triacanthella sp. 2	0	0	0	0	0	0	37	33	0	0	0	0
Triacanthella sp. 3	0	0	209	51	0	0	0	0	0	0	0	0
Triacanthella cf. madiba	3	1	0	0	0	0	0	0	0	0	0	0

	EP	PP	EM	PM	EW	PW	EK	PK	EJ	PJ	EB	PB
Willemia sp. 1	0	0	0	0	0	0	0	1	0	0	0	0
Willemia sp. 2	0	0	0	0	1	4	0	0	0	0	0	0
Xenylla sp.	0	0	164	14	1	0	24	14	0	0	0	0
Neanuridae												
Aethiopella sp.	3	4	0	0	0	0	0	0	0	2	2	0
cf. Aethiopella sp.	0	0	0	0	1	0	0	0	0	0	0	0
cf. Tasmanura sp.	0	0	0	0	0	0	0	0	1	1	0	0
Ectonura sp. 1	0	0	0	0	0	0	0	0	4	4	0	0
Ectonura sp. 2	0	0	46	4	0	0	0	0	0	0	0	0
Friesea sp.	0	0	0	0	0	0	0	0	0	0	0	122
Micranurida sp. 1	0	0	0	0	0	0	7	2	0	0	0	0
Micranurida sp. 2	0	0	1	2	0	0	0	0	0	0	0	0
Micranurida sp. 3	1	18	0	0	0	0	0	0	0	0	0	0
Neanura cf.muscorum	0	0	0	3	0	0	2	10	0	0	0	0
Neanuridae sp.	1	0	0	0	0	0	0	0	0	0	0	0
Pseudachorutes sp. 1	0	0	0	0	0	0	56	9	0	0	0	0
Pseudachorutes sp. 2	0	0	13	6	0	0	0	0	0	0	0	0
Pseudachorutes sp. 3	7	5	0	0	0	0	0	0	0	0	0	0
Pseudachorutes sp. 4	0	0	0	0	31	10	0	0	0	0	0	0
Pseudochorutes sp. 5	0	0	0	0	0	0	0	0	7	3	1	0
Odontellidae												
cf. *Afrodontella* sp.	1	1	0	0	0	0	0	0	0	0	0	0
Odontellidae sp.	0	0	0	0	0	0	0	1	0	0	0	0
Tullbergiidae												
Mesaphorura sp. 1	0	0	0	0	4	59	7	13	22	3	0	0
Mesaphorura sp. 2	0	0	1	2	0	0	0	0	0	0	0	0
Mesaphorura sp. 3	2	0	0	0	0	0	0	0	0	0	0	0
Tullbergia sp. 1	0	0	0	0	0	0	0	0	0	0	0	2
Tullbergia sp. 2	0	0	0	0	0	0	0	0	2	0	0	0
Tullbergia sp. 3	0	0	0	0	0	0	2	17	0	0	0	0
Tullbergia sp. 4	0	0	3	2	0	0	0	0	0	0	0	0
Tullbergia sp. 5	4	3	0	0	0	0	0	0	0	0	0	0
Tullbergia sp. 6	0	0	0	0	42	47	0	0	0	0	0	0
Order Symphypleona												
Bourletiellidae												
Bourletiellidae sp. 1	0	0	0	0	0	0	0	0	0	0	0	1
Bourletiellidae sp. 2	0	0	0	0	0	0	0	0	1	1	0	0
Dicyrtomidae												
Dicyrtomidae sp. 1	0	0	0	0	0	0	3	3	0	0	0	0
Dicyrtomidae sp. 2	0	0	0	1	0	0	0	0	0	0	0	0
Katiannidae												
Sminthurinus sp. 1	0	0	0	0	7	36	0	0	0	0	0	0
Sminthurinus sp. 2	0	0	0	0	0	0	0	0	7	2	0	0

	EP	PP	EM	PM	EW	PW	EK	PK	EJ	PJ	EB	PB
Sminthurinus sp. 3	0	0	0	0	0	0	0	0	35	46	0	0
Sminthurinus sp. 4	0	0	0	0	0	2	0	0	0	0	0	0
Sminthurinus sp. 5	0	0	0	0	11	21	0	0	0	0	0	0
Sminthurinus sp. 6	0	0	0	5	0	0	0	0	0	0	0	0
Sminthurinus sp. 7	0	0	0	0	0	0	29	8	0	0	0	0
Sminthurinus sp. 8	13	28	97	23	0	0	0	0	0	0	0	0
Sminthurinus sp. 9	0	0	0	0	0	0	0	0	0	0	6	0
Sminthurinus sp. 10	0	0	0	0	0	0	0	0	0	0	1	16
Sminthuridae												
Sminthuridae sp. 1	0	0	0	0	0	0	0	1	0	0	0	0
Sminthuridae sp. 2	1	0	0	0	0	0	0	0	0	0	0	0
Sminthurididae												
Sphaeridia sp. 1	0	0	0	0	0	0	0	0	4	20	0	0
Sphaeridia sp. 2	103	52	0	0	16	6	19	9	0	0	0	0

Table 3: Results from a generalized linear model showing the effect of litter type, site and decomposition rate (k) on Collembola (A) species richness (n=148) and (B) abundance in Jonkershoek Nature Reserve. No interactions were significant and were therefore omitted from the final models.

(A)

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Litter EP	0.124138	1.463	1.463	ns
Litter *Galenia*	0.293639	0.081754	3.592	***
Litter *Protea*	0.195910	0.084125	2.329	*
Litter *Restio*	0.203691	0.083349	2.444	*
Site *Protea*	0.001281	0.062000	0.021	ns
Site *Restio*	-.029414	0.061869	-0.475	ns

(B)

	Estimate	**s.e.**	**t-value**	**p**
Abundance				
Litter EP	0.8616	0.3258	2.645	**
Litter *Galenia*	1.1112	0.3152	3.526	***
Litter *Protea*	0.8592	0.3275	2.624	**
Litter *Restio*	0.6255	0.3381	1.850	ns
Site *Protea*	-0.3494	0.1892	-1.847	ns
Site *Restio*	-0.8821	0.2227	-3.962	***

Table 4: Results from generalized linear models investigating the effect of vegetation type (i.e. *Erica* vs. *Protea* site), litter type and site on (A) species richness and (B) abundance between different sites (JNK = Jonkershoek, KOG= Kogelberg, MTR = Mont Rochelle, PEN = Peninsula and WIL = Wilderness).

(A)

	Estimate	**s.e.**	**t-value**	**p**
Species richness				
Litter *Galenia*	0.96758	0.21316	4.539	***
Site JNK	1.78295	0.19612	9.091	***
Site KOG	1.93836	0.19408	9.988	***
Site MTR	1.96084	0.19381	10.117	***
Site PEN	1.86903	0.19564	9.554	***
Site WIL	1.70952	8.669	8.669	***
Litter *Galenia* x Site JNK	-0.94138	0.23742	--3.965	***
Litter *Galenia* x Site KOG	-0.90163	0.23370	-3.858	***
Litter *Galenia* x Site MTR	-1.09374	0.23522	-4.650	***
Litter *Galenia* x Site PEN	-0.84696	0.23564	-3.594	***
Litter *Galenia* x Site WIL	-0.75855	0.23892	-3.175	**

(B)

	Estimate	**s.e.**	**t-value**	**p**
Abundance				
Litter *Galenia*	0.1582	0.1280	1.236	ns
Site JNK	2.3019	0.5140	4.479	***
Site KOG	2.1696	0.5173	4.194	***
Site MTR	2.0454	0.5208	3.928	***
Site PEN	3.2041	0.5004	6.403	***
Site WIL	2.1964	0.5189	4.232	***
Veg *Protea*	0.1530	0.1279	1.197	ns

Figures

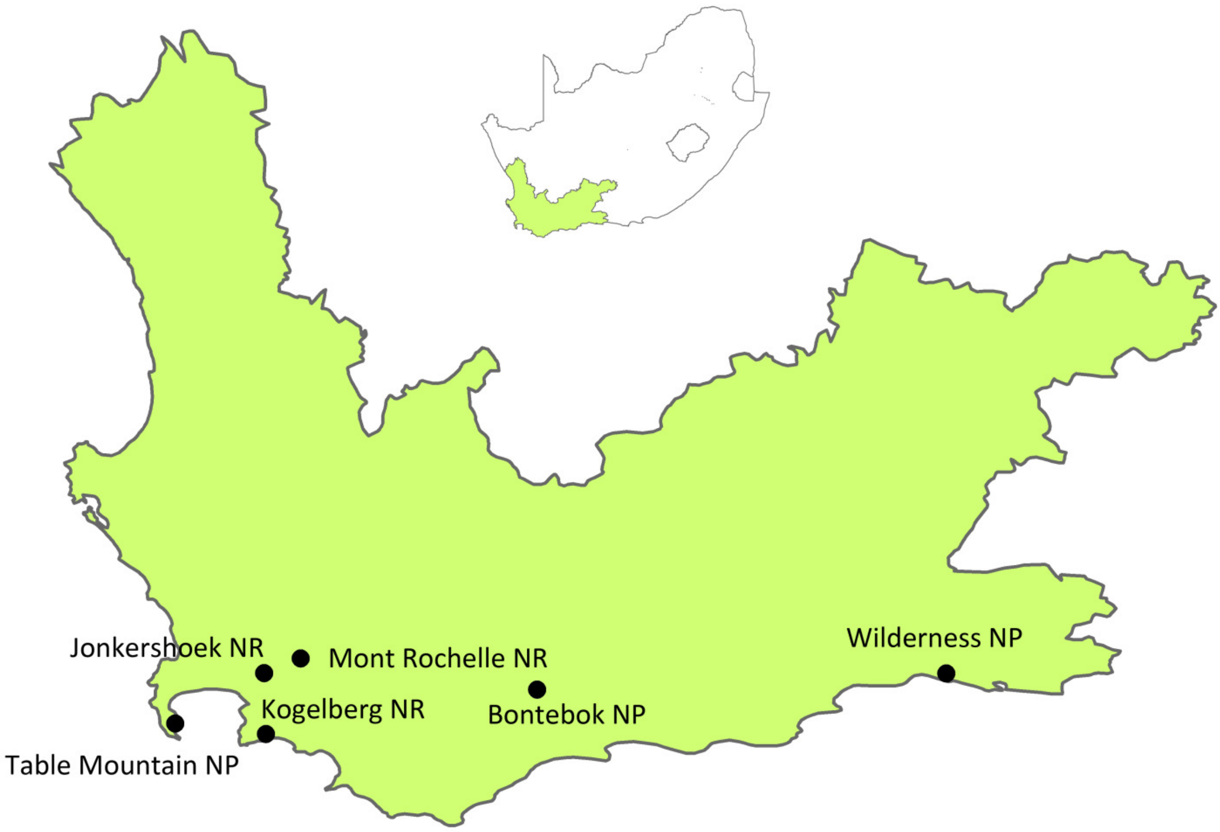


Fig. 1A: Map of the sites used in the study (NP=National Park, NR=Nature Reserve). Map by B. Coetzee.

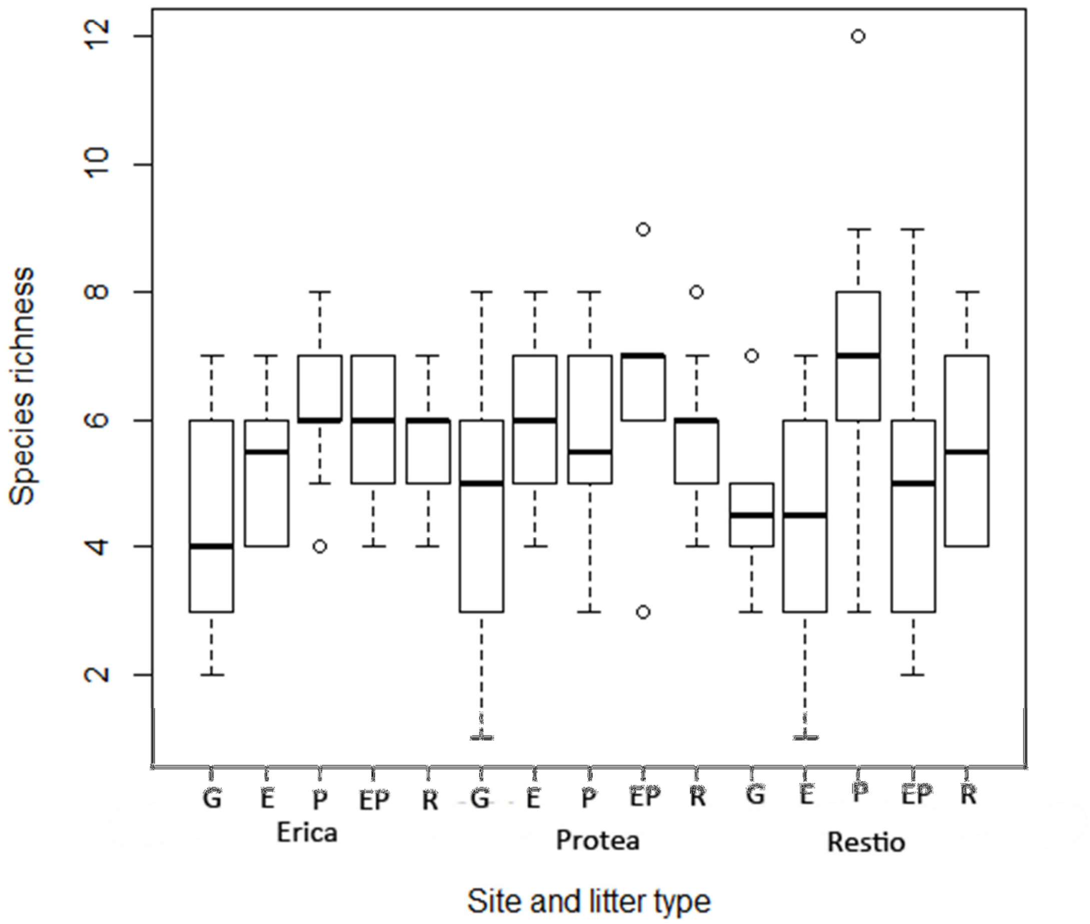


Fig 2A: Springtail species richness in Jonkershoek Nature Reserve as a factor of site and litter type (n=30 each). For litter type, G=*Galenia*, E=*Erica*, P=*Protea*, EP=*Erica-Protea* mixture, R=*Restio*.

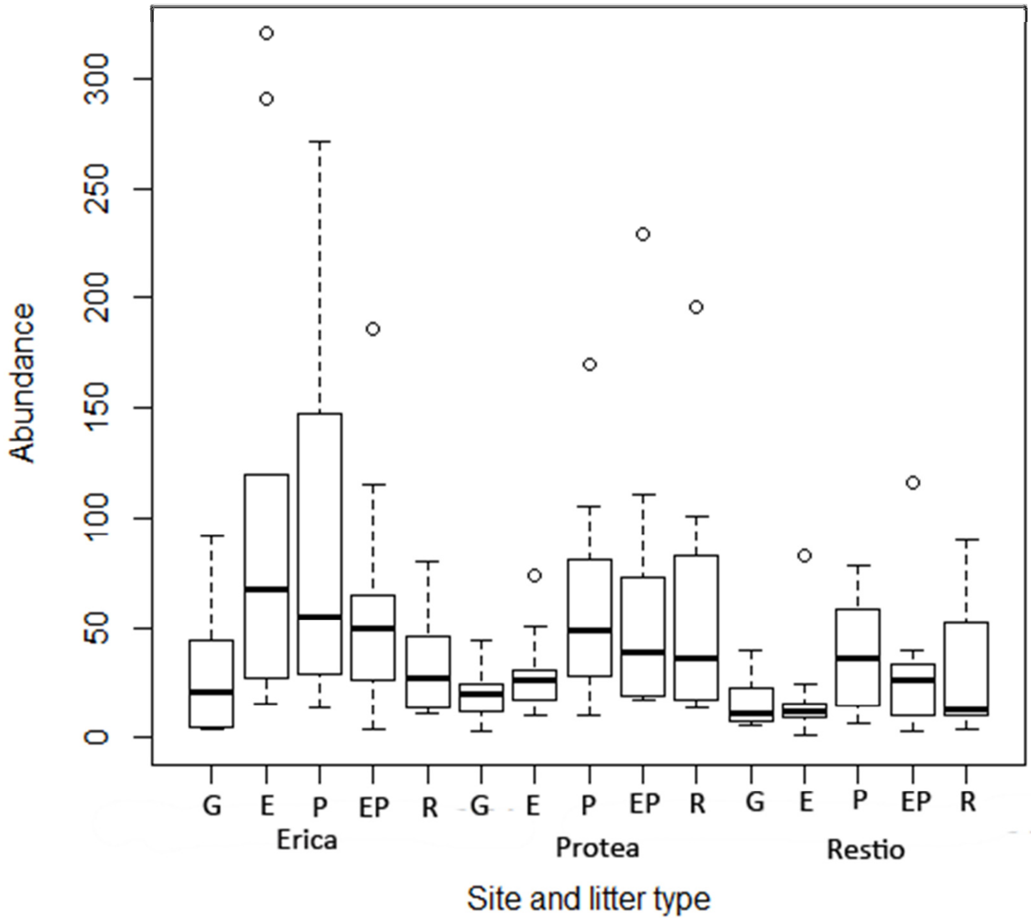


Fig 2B: The effect of litter type and site springtail abundance in Jonkershoek Nature Reserve (n=30 each). For litter type, G=*Galenia*, E=*Erica*, P=*Protea*, EP=*Erica-Protea* mixture, R=*Restio*.

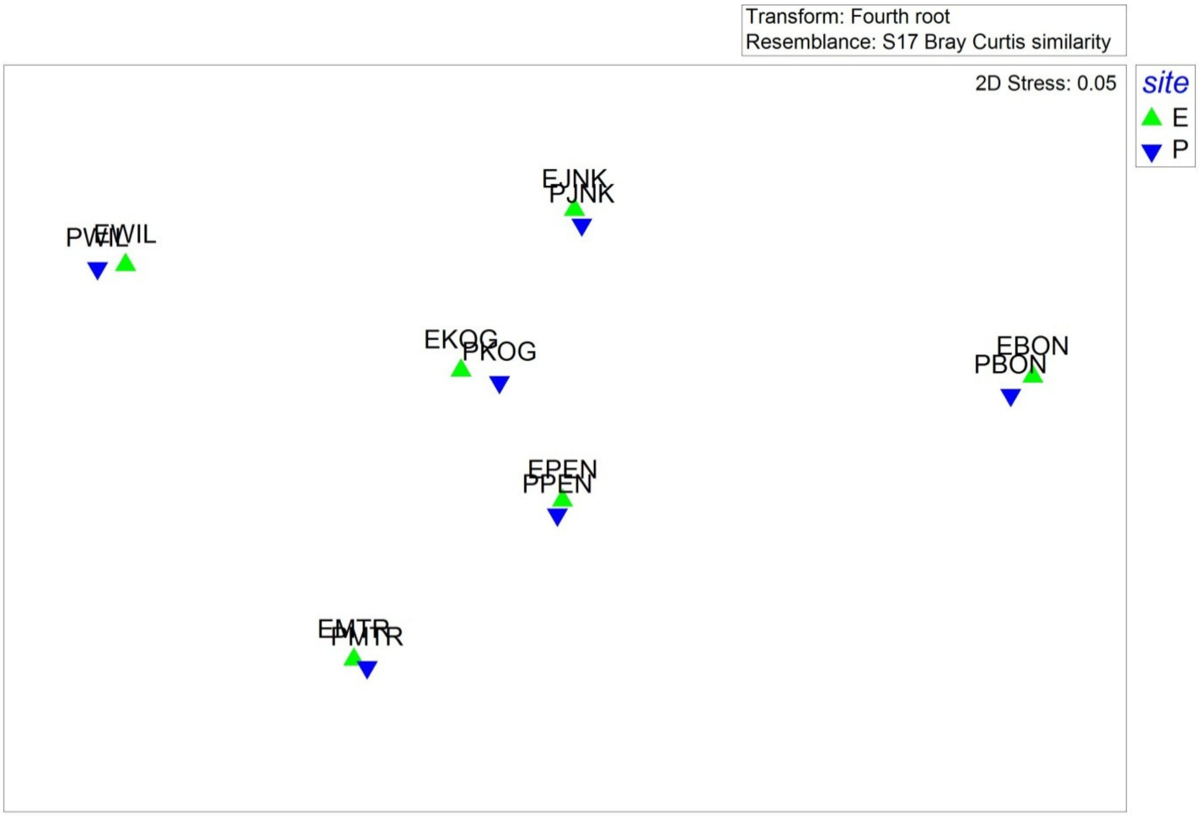


Fig. 3: Non-metric multidimensional scaling plot of the assemblages between sites. E=Erica site, P=Protea site, BON=Bontebok, WIL=Wilderness, MTR=Mont Rochelle, PEN=Peninsula, JNK=Jonkershoek, KOG=Kogelberg.

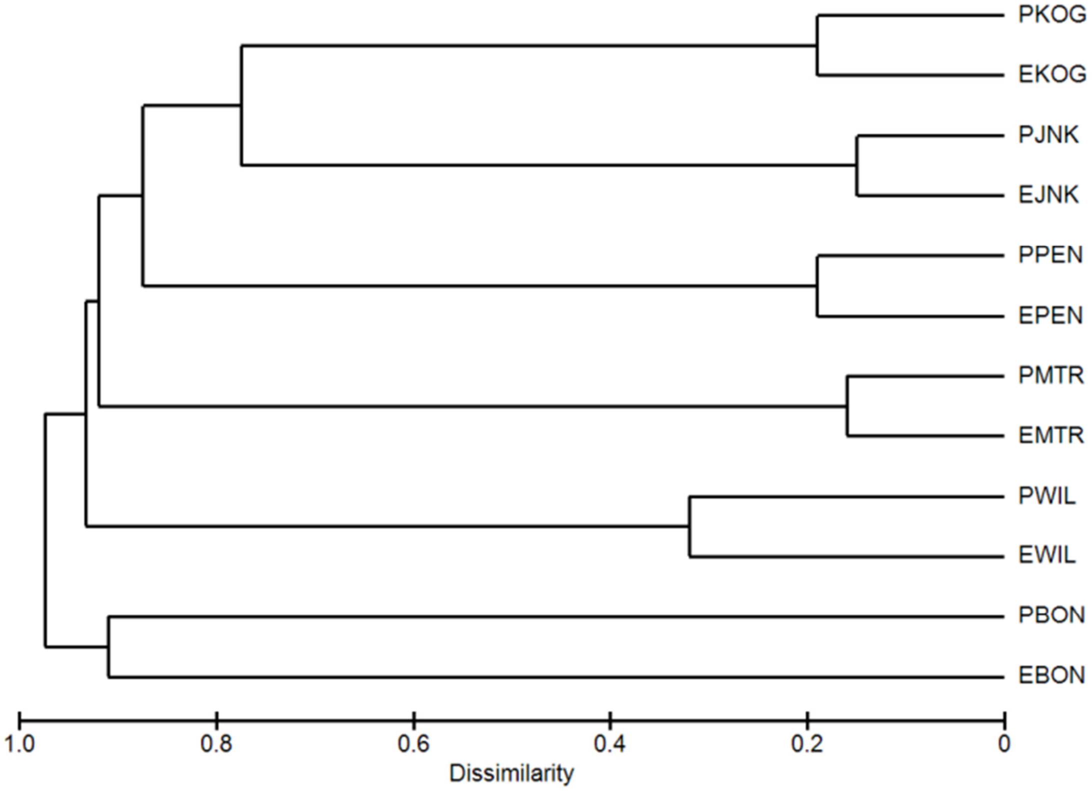


Fig. 4A: Dendrogram showing the dissimilarity between sites using beta diversity measurements, B_{cc}. E=*Erica* site, P=*Protea* site, BON=Bontebok, WIL=Wilderness, EMTR=Mont Rochelle, PEN=Peninsula, JNK=Jonkershoek, KOG=Kogelberg.

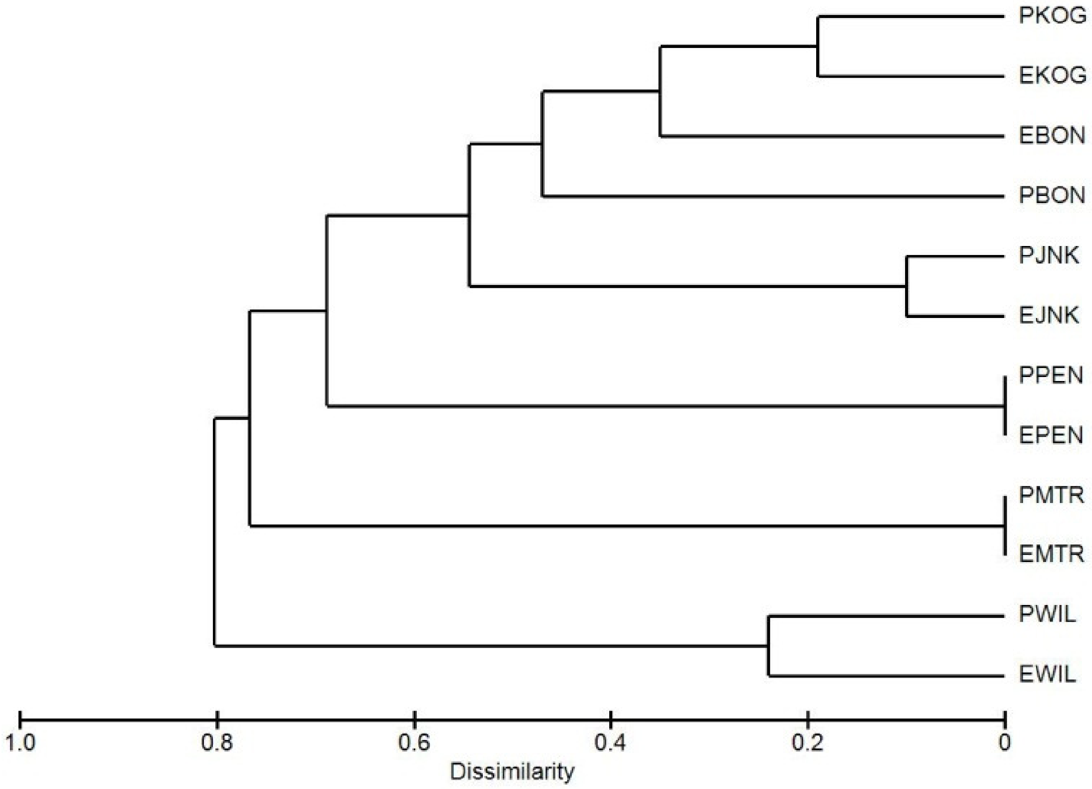


Fig. 4B: Dendrogram showing the dissimilarity between sites using beta diversity measurements, B_{-3}. E=*Erica* site, P=*Protea* site, BON=Bontebok, WIL=Wilderness, EMTR=Mont Rochelle, PEN=Peninsula, JNK=Jonkershoek, KOG=Kogelberg.

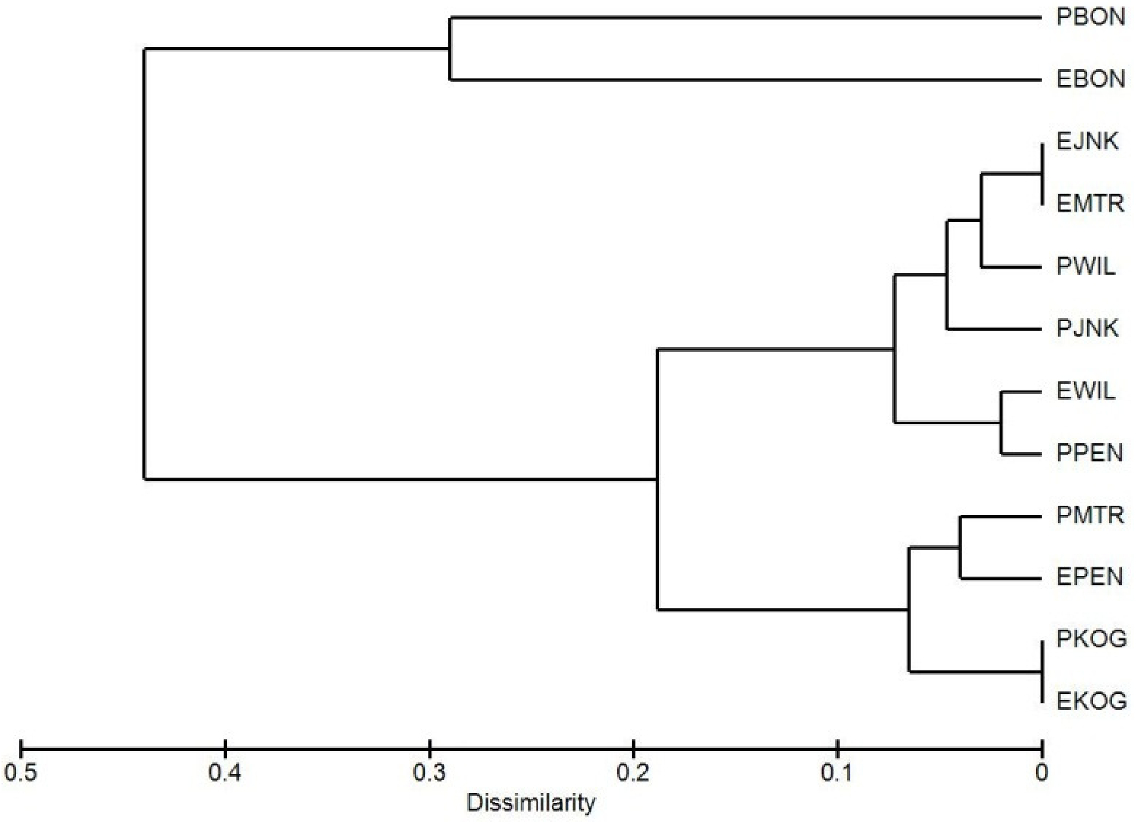


Fig. 4C: Dendrogram showing the dissimilarity between sites using beta diversity measurement B_{rich}. E=*Erica* site, P=*Protea* site, BON=Bontebok, WIL=Wilderness, EMTR=Mont Rochelle, PEN=Peninsula, JNK=Jonkershoek, KOG=Kogelberg.

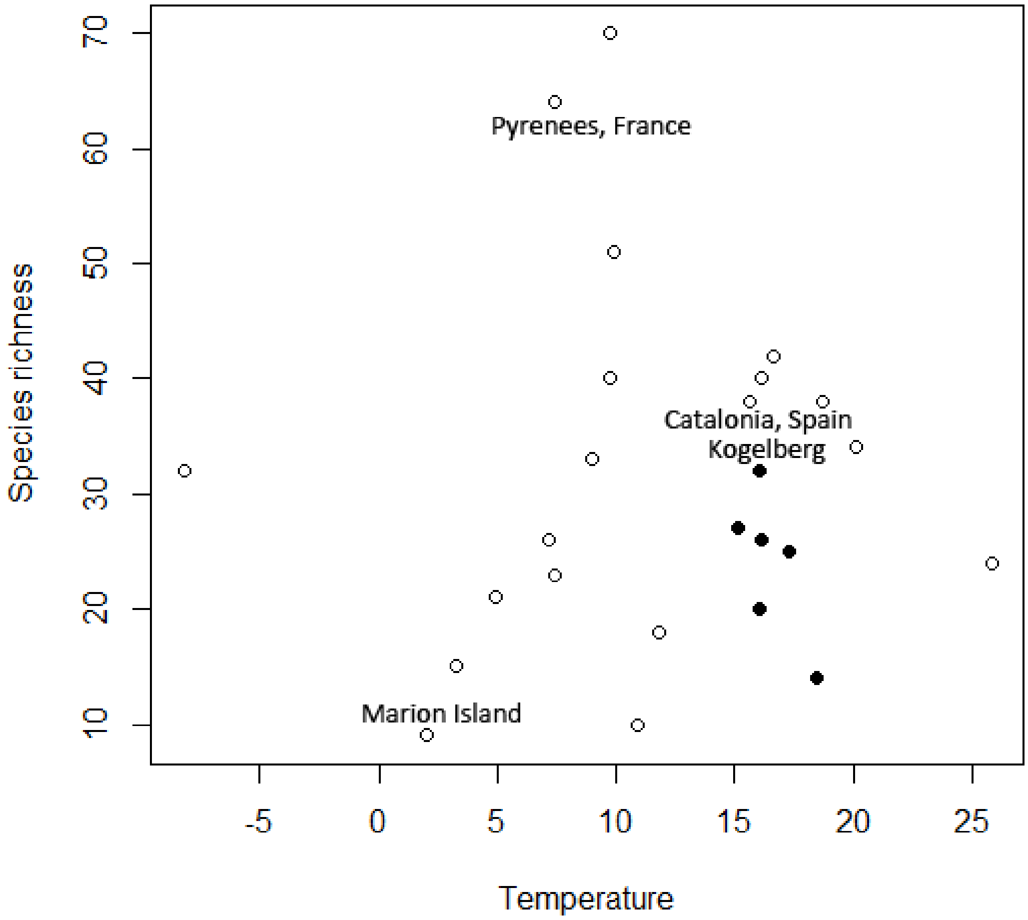


Fig. 5: Species richness (local) vs. mean annual temperature (°C) from this study and other studies (closed circles are values from this study).

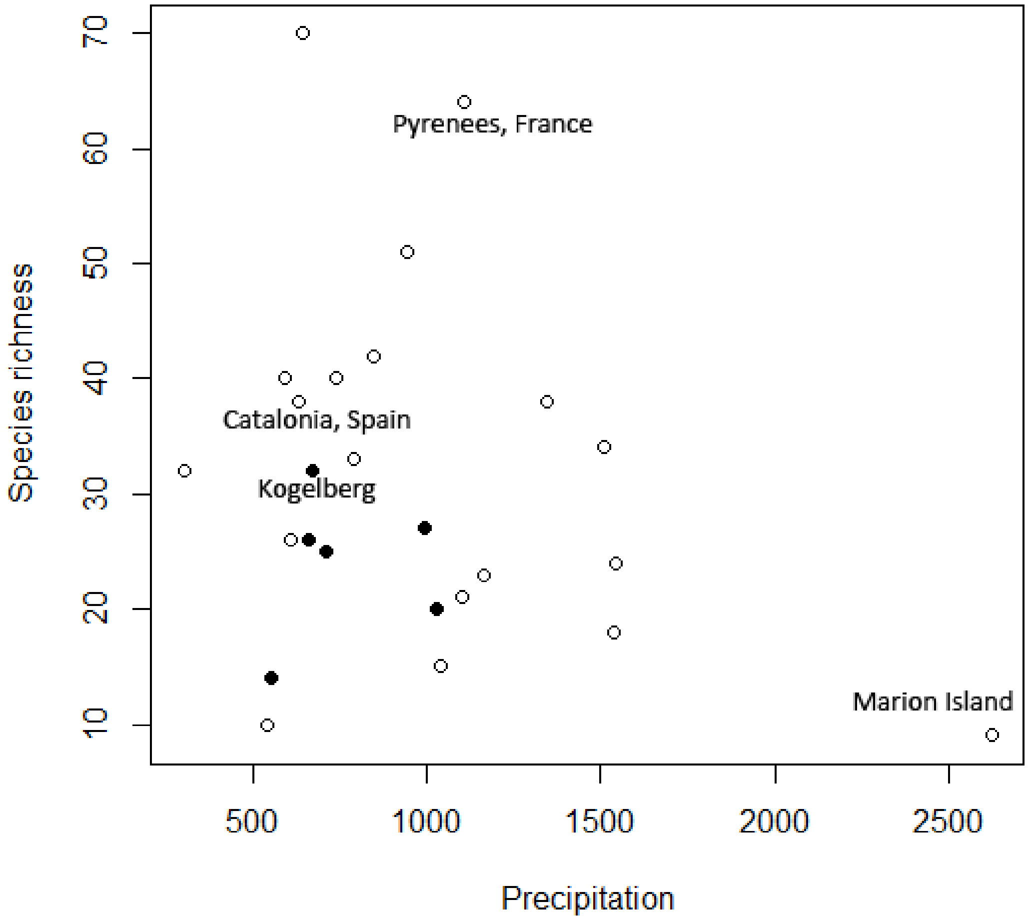


Fig. 6: Species richness vs. precipitation (mm) from this study and other studies (closed circles are values from this study).

Supplementary material
Tables

Table 1: Study sites coordinates.

Site	Nearest town	Latitude	Longitude
Bontebok National Park	Swellendam	-34.078417°	20.467111°
Cape Peninsula, Table Mountain National Park	Cape Town	-34.260111°	18.393361°
Mont Rochelle Nature Reserve	Franschhoek	-33.903389°	19.159000°
Garden Route National Park	Sedgefield	-33.991606°	22.734903°
Jonkershoek Nature Reserve	Stellenbosch	-33.988646°	18.95519°
Kogelberg Nature Reserve	Kleinmond	-34.324817°	18.965033°

Table 2: A dissimilarity matrix for B_{rich} and B_{-3}.

B_{-3} B_{rich}	EPEN	PPEN	EMTR	PMTR	EWIL	PWIL	EKOG	PKOG	EJNK	PJNK	EBON	PBON
EPEN		0	0.76	0.87	0.87	0.82	0.83	0.86	0.7	0.67	0.38	0.56
PPEN	0.19		0.86	0.83	0.93	0.92	0.78	0.76	0.83	0.76	0.44	0.69
EMTR	0.17	0.05		0	0.87	0.95	0.7	0.7	0.94	0.91	0.54	0.73
PMTR	0.04	0.07	0.16		0.91	0.88	0.81	0.91	0.83	0.8	0.45	0.63
EWIL	0.09	0.02	0.08	0.05		0.24	0.76	0.78	0.84	0.86	0.48	0.67
PWIL	0.14	0.03	0.03	0.09	0.08		0.73	0.76	0.89	0.86	0.52	0.76
EKOG	0.04	0.1	0.21	0.09	0.13	0.18		0.19	0.53	0.53	0.35	0.49
PKOG	0.04	0.16	0.21	0.09	0.13	0.18	0		0.53	0.53	0.35	0.49
EJNK	0.18	0.06	0	0.12	0.08	0.03	0.24	0.24		0.1	0.42	0.69
PJNK	0.81	0.09	0.03	0.15	0.11	0.06	0.26	0.26	0.05		0.36	0.76
EBON	0.59	0.52	0.46	0.55	0.52	0.48	0.62	0.62	0.5	0.5		0.43
PBON	0.42	0.31	0.27	0.37	0.33	0.29	0.46	0.46	0.28	0.24	0.29	

Table 3: Summary of studies from the literature and the environmental variables obtained.

Site name	No. species	Mean Temp (°C)	Mean rainfall (mm)	Reference
Marion Island (sub-Antarctic)	9	2	2625	Gabriel et al. 2001
Oldebroek, Netherlands	10	10.9	537	Petersen 2011
Bontebok, South Africa	14	18.4	547	This study
Macquarie Island (sub-Antarctic)	15	3.3	1040	Terauds et al. 2011
Malaleuca, Tasmania	18	11.8	1535	Greenslade & Smith 1999
Jonkershoek, South Africa	20	16	1029	This study
Quebec City, Canada	21	4.9	1099	Rochefort et al. (2006)
Clocaenog, Wales,UK	23	7.4	1163	Petersen 2011
Guaju , Brazil	24	25.8	1541	Zeppelini et al. (2009)
Wilderness, South Africa	25	17.3	707	This study
Mols, Denmark	26	7.2	609	Petersen 2011
Peninsula, South Africa	26	16.1	658	This study
Mont Rochelle, South Africa	27	15.1	993	This study
Spitsbergen, Svalbard	32	-8.2	298	Uvarov and Byzova 1995
Kogelberg, South Africa	32	16	667	This study
Oldebroek, Netherlands	33	9	789	Petersen 2011
Tokai, South Africa	34	20.1	1508	Liu et al. 2012
Catalonia, Spain	38	15.6	628	Petersen 2011
Espirito Santo, Brazil	38	18.7	1344	Culik et al. 2002
Rouen, France	40	9.7	736	Chauvat et al. 2011
Sardinia, Italy	40	16.1	592	Petersen 2011
Tokai, South Africa	42	16.6	845	Liu et al. 2012
Bethmale, France	51	9.9	940	Cassagne et al. (2006)
Gar-Cagire, France	64	7.4	1103	Salmon et al. (2010)
Vienna, Austria	70	9.7	640	Querner & Bruckner (2010)

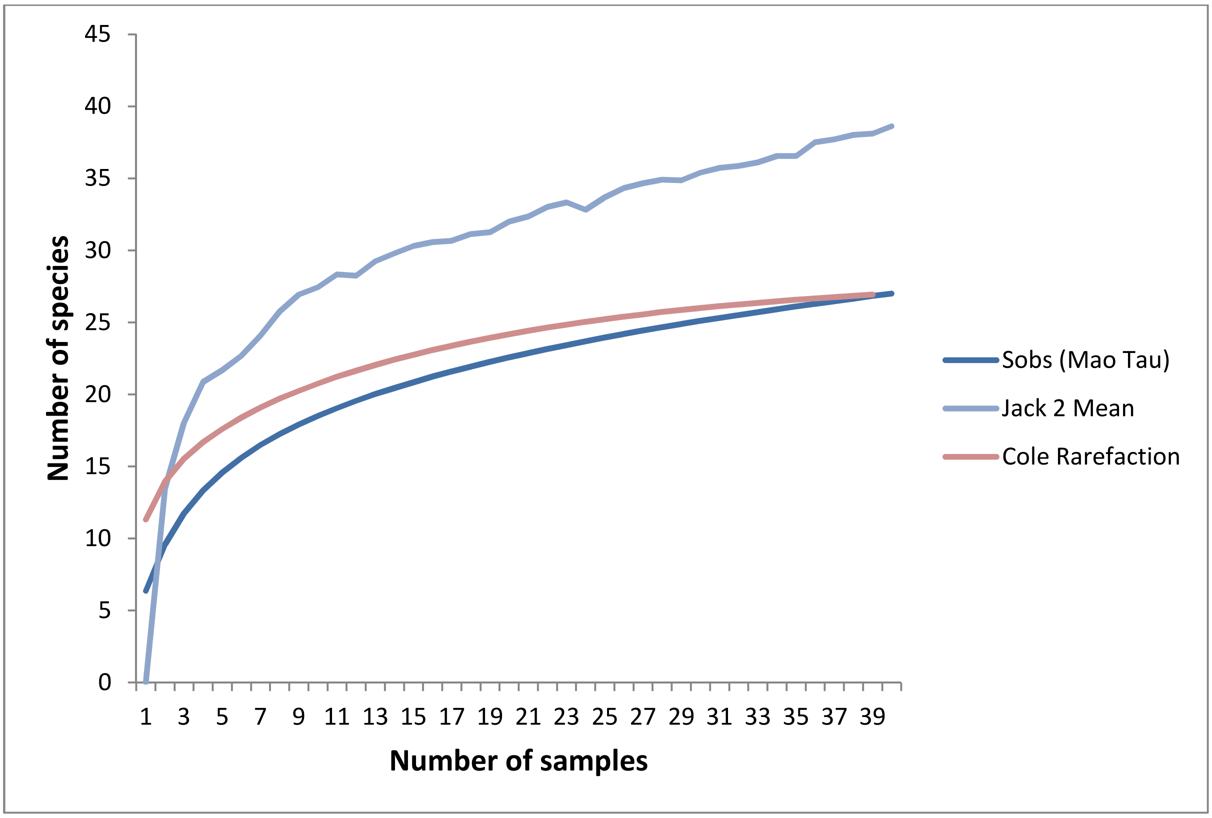


Fig. 1A: Species accumulation curve for Mont Rochelle.

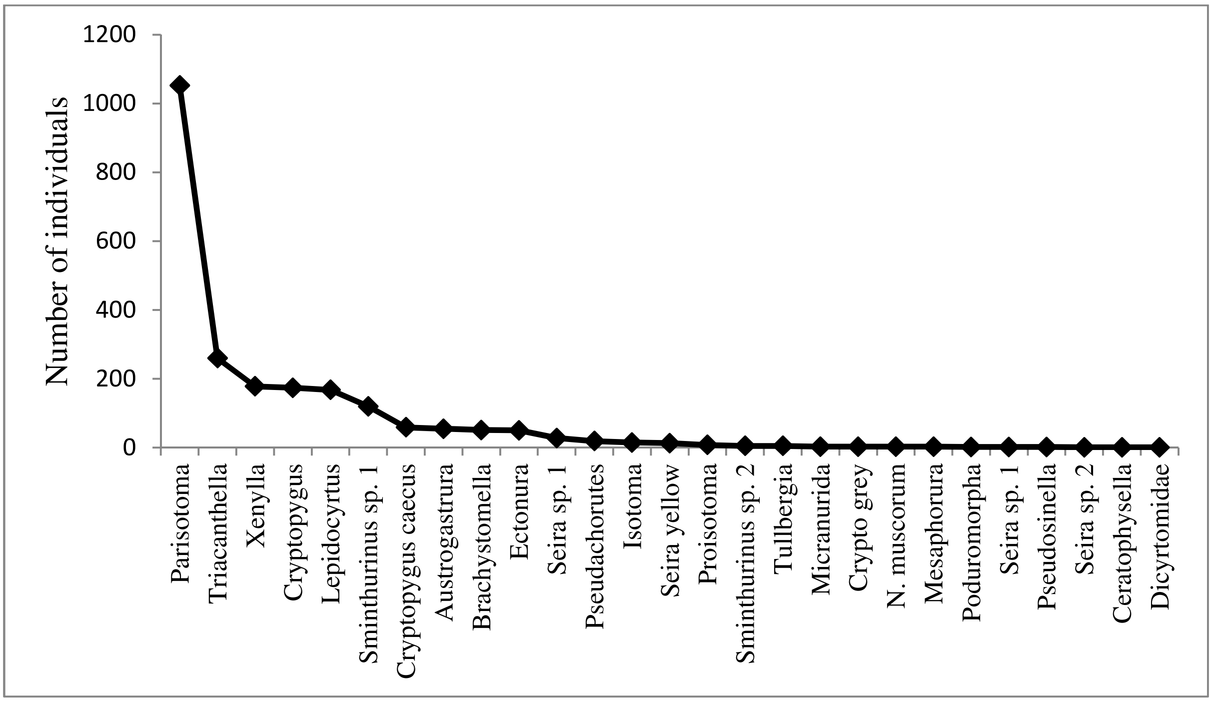


Fig. 1B: Species rank abundance curve for Mont Rochelle.

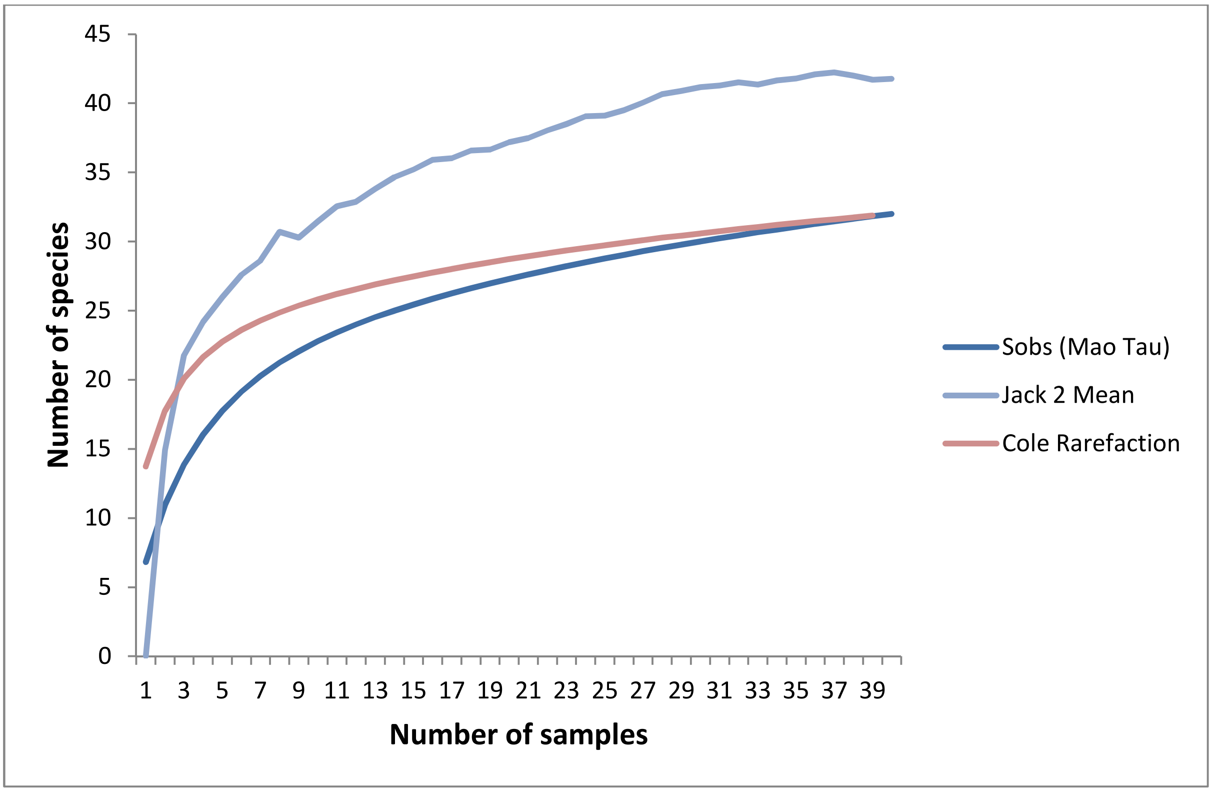


Fig. 2A: Species accumulation curve for Kogelberg.

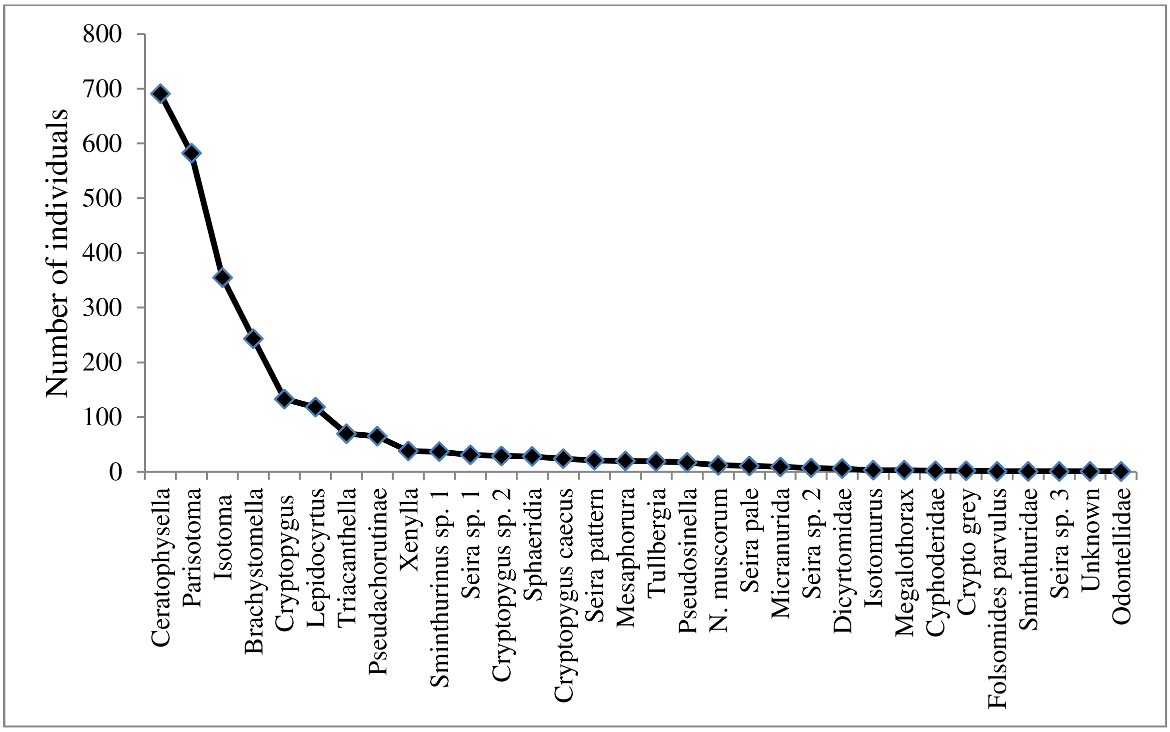


Fig. 2B: Species rank abundance curve for Kogelberg.

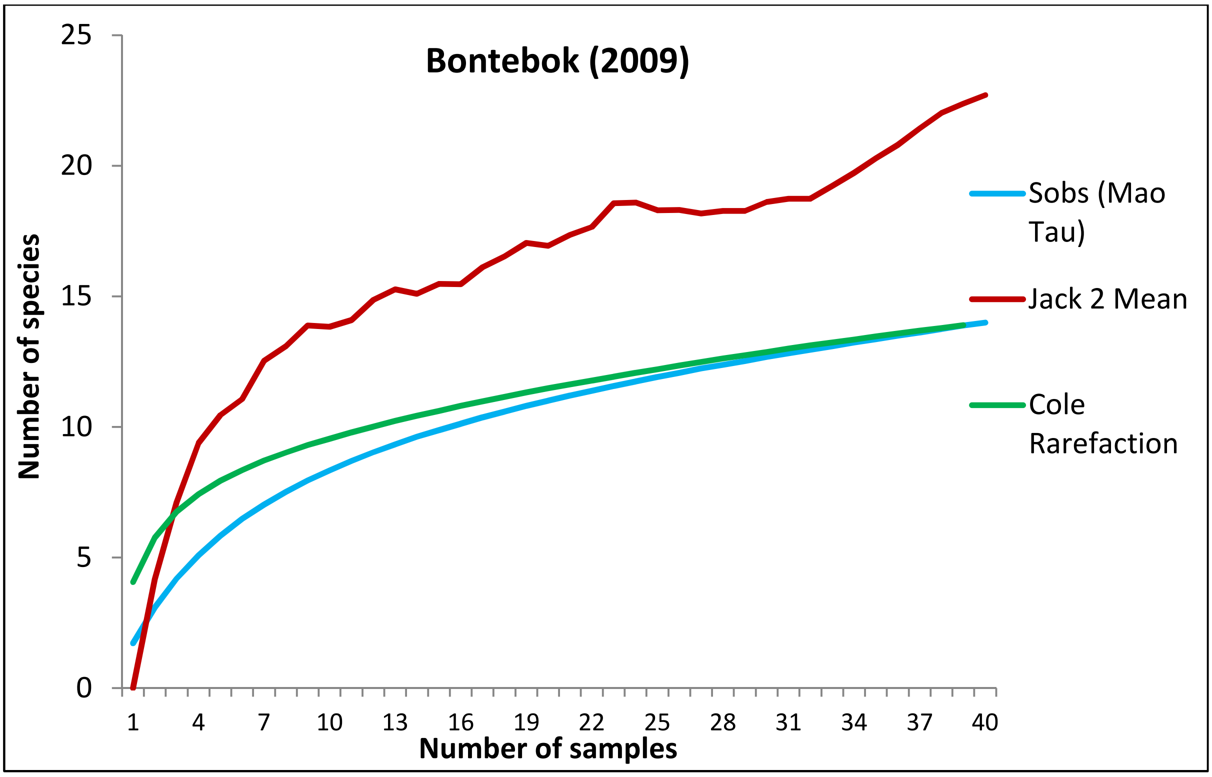


Fig. 3A: Species accumulation curve for Bontebok.

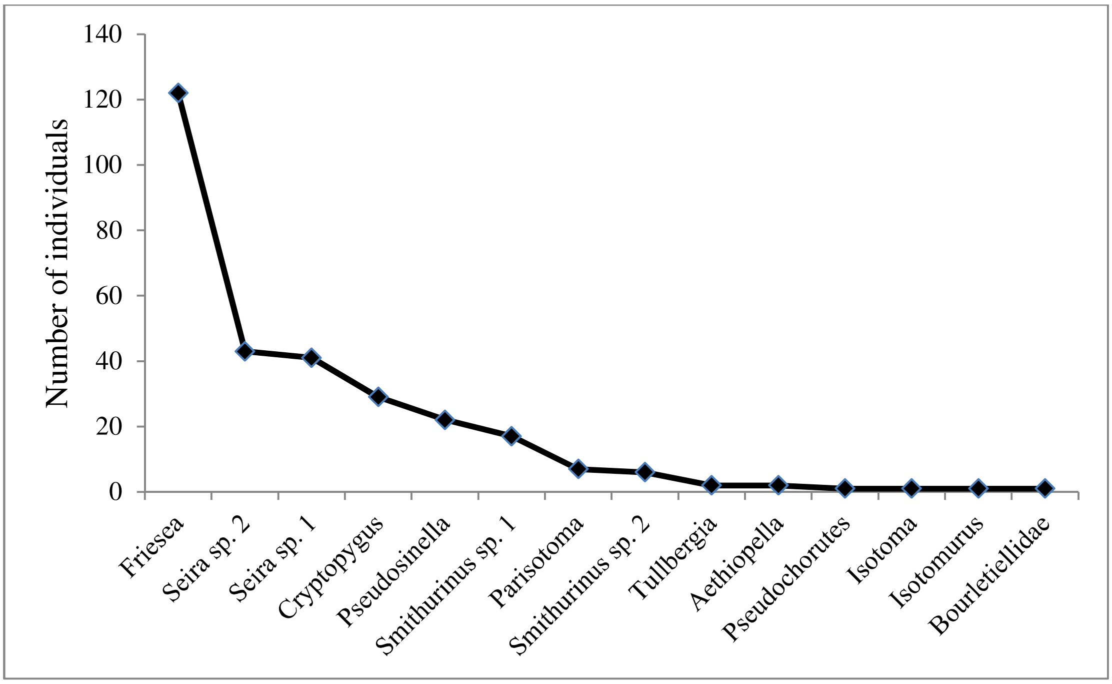


Fig. 3B: Species rank abundance curve for Bontebok.

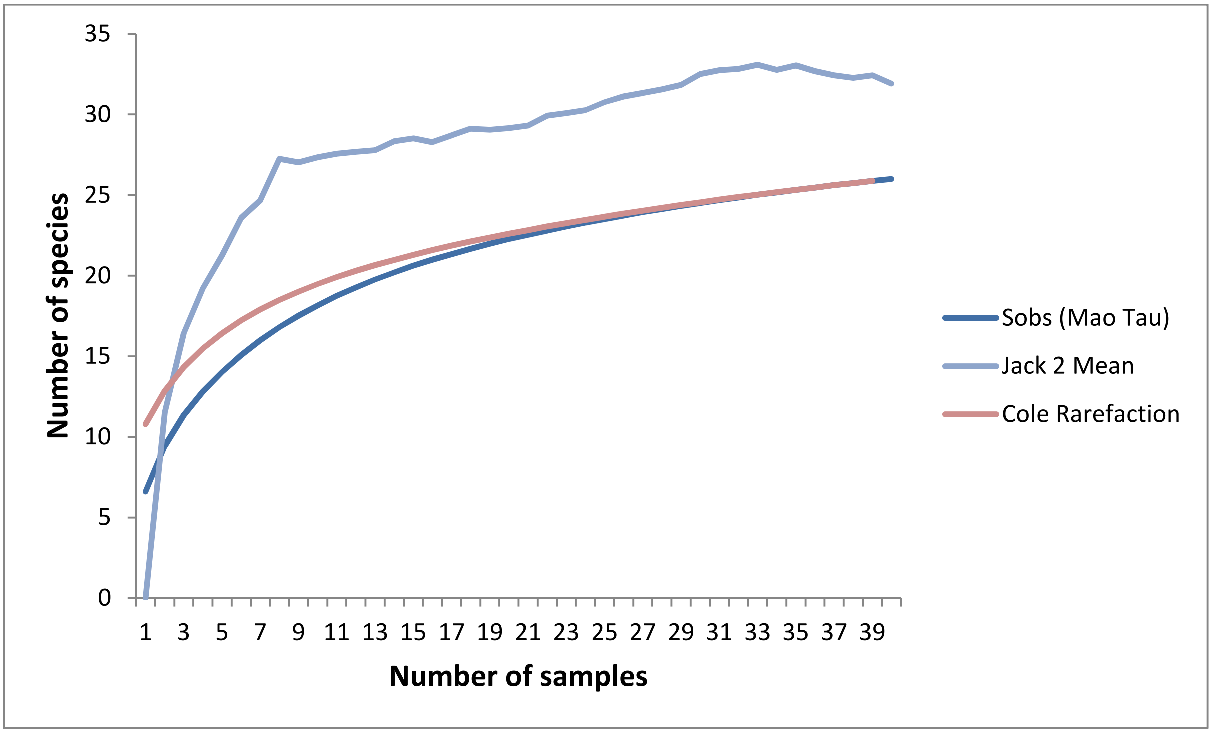


Fig. 4A: Species accumulation curve for Peninsula.

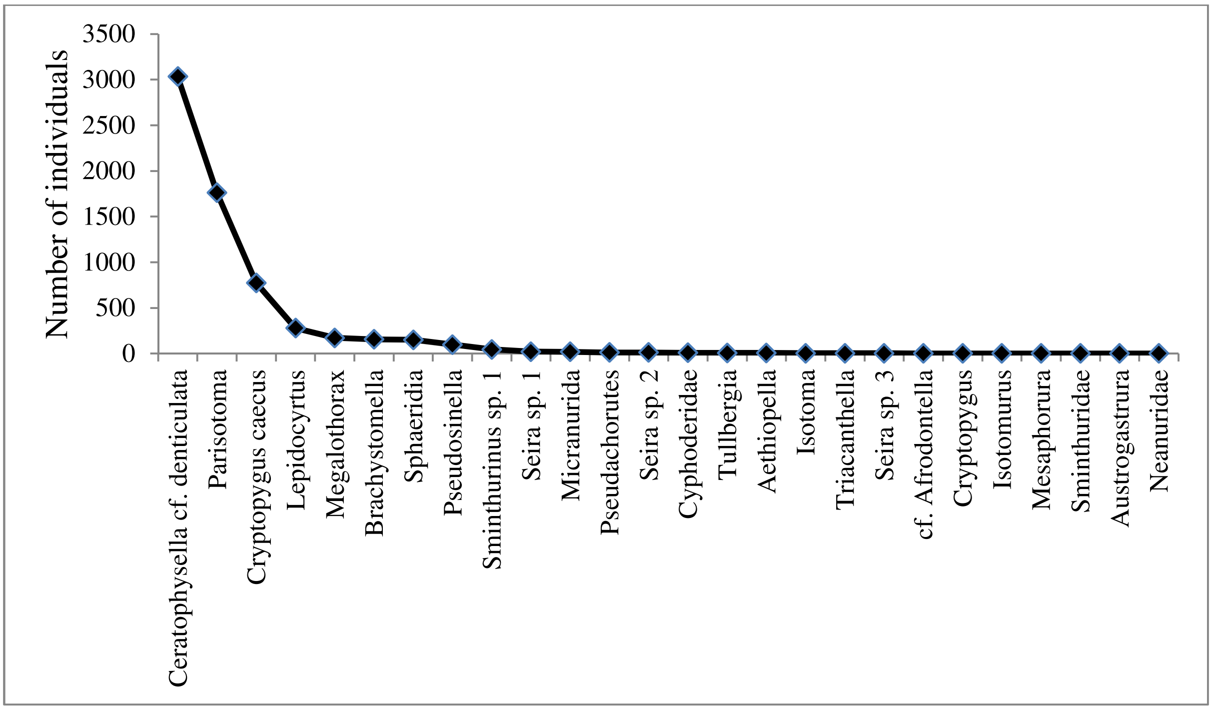


Fig. 4B: Species rank abundance curve for Peninsula.

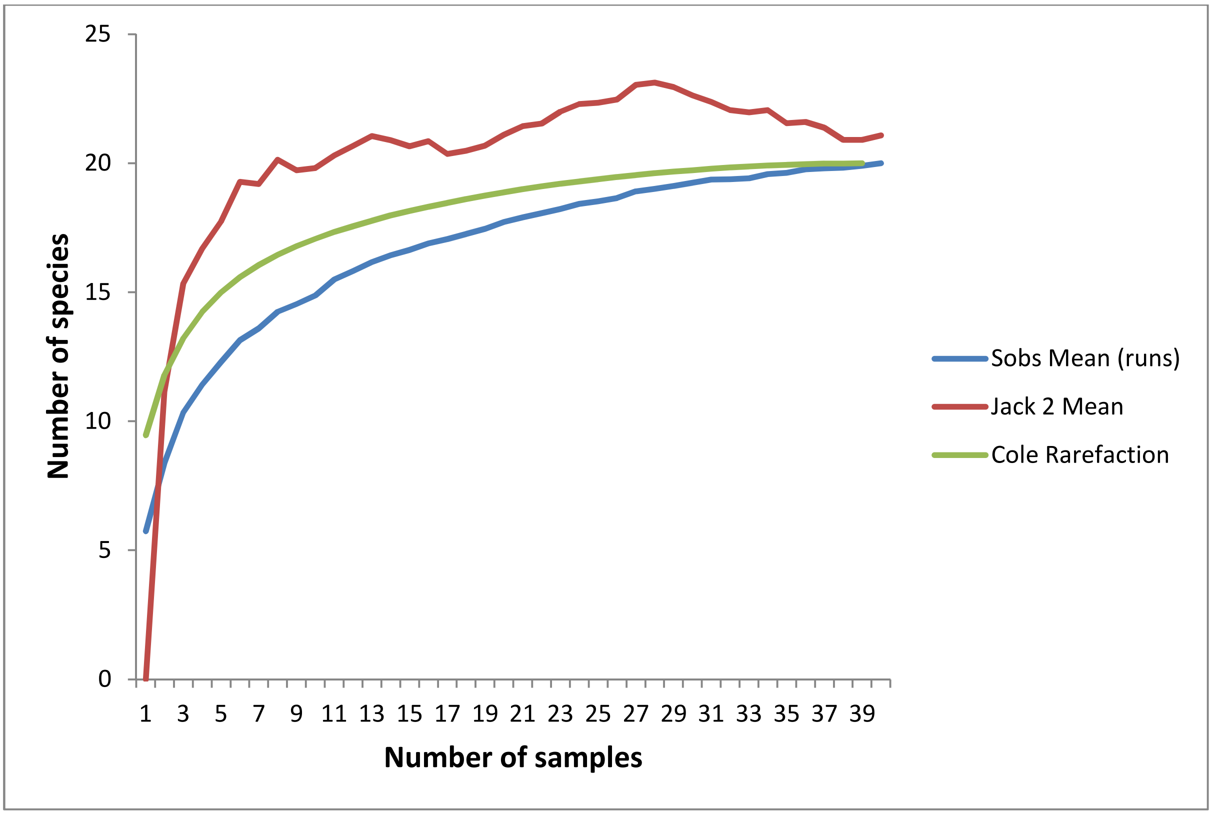


Fig. 5A: Species accumulation curve for Jonkershoek.

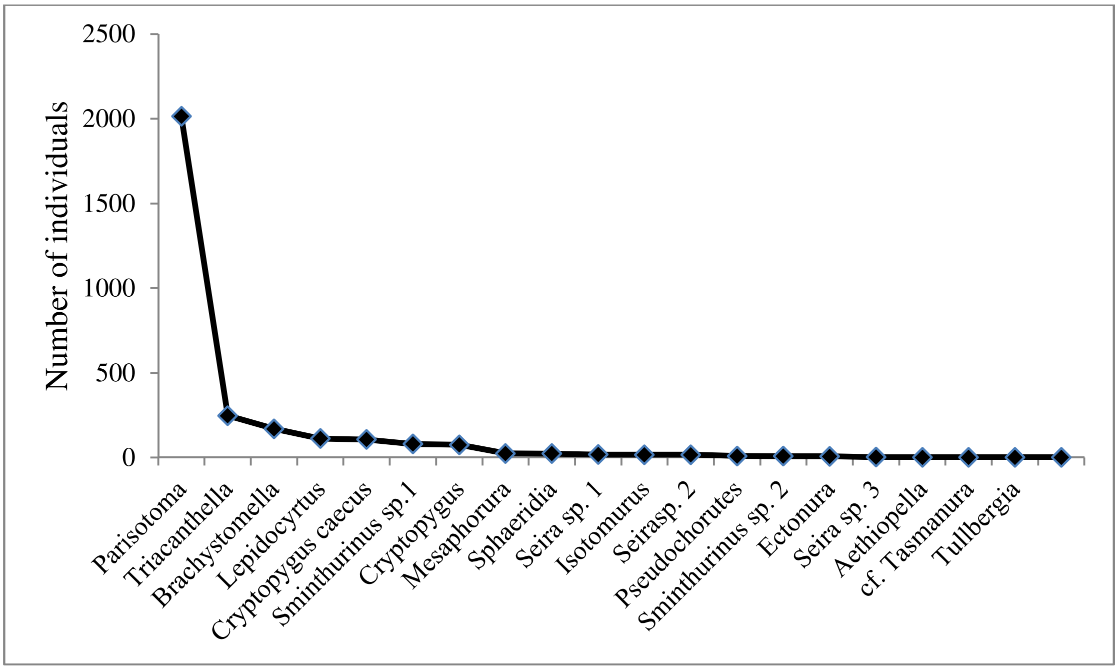


Fig. 5B: Species rank abundance curve for Jonkershoek.

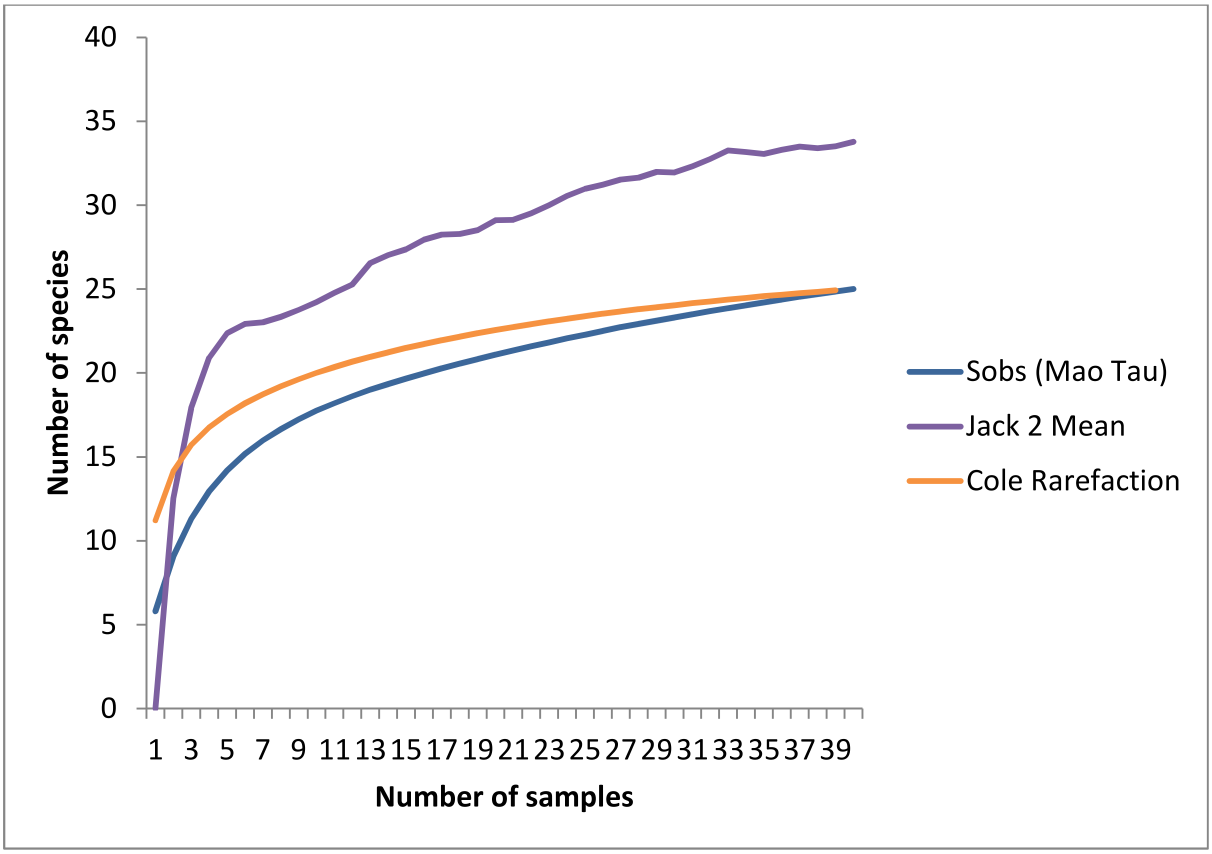


Fig. 6A: Species accumulation curve for Wilderness.

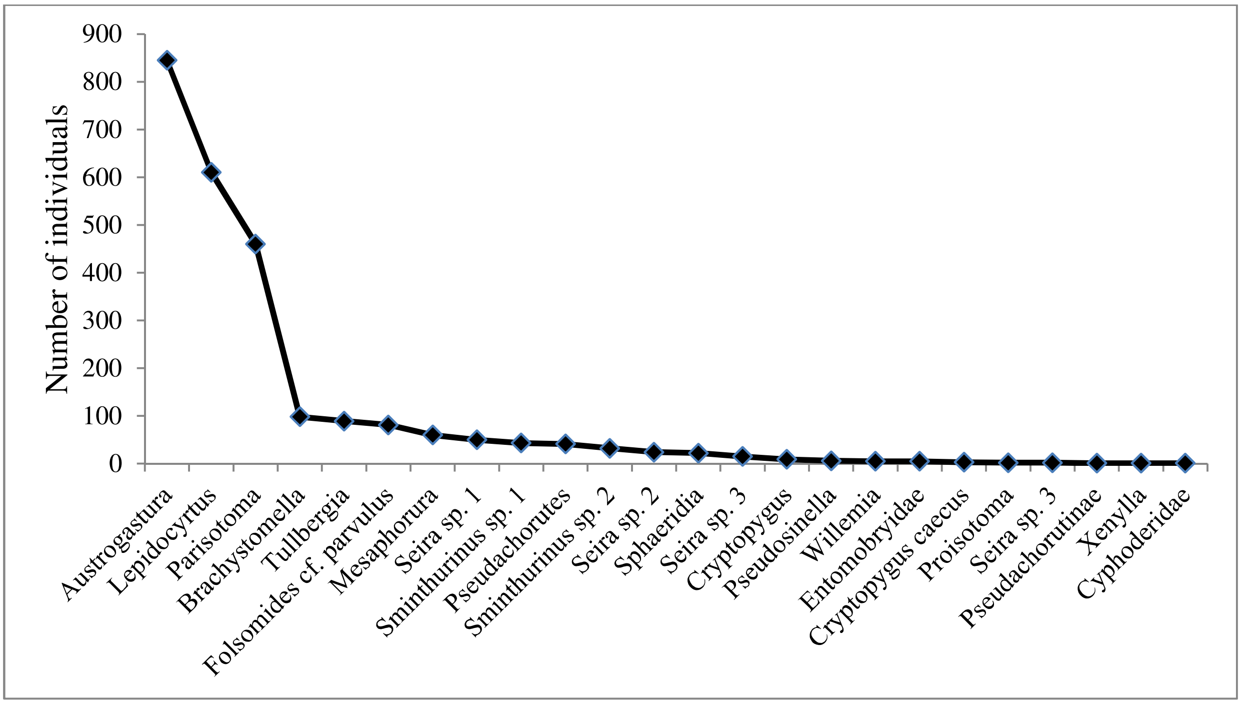


Fig. 6B: Species rank abundance curve for Wilderness.

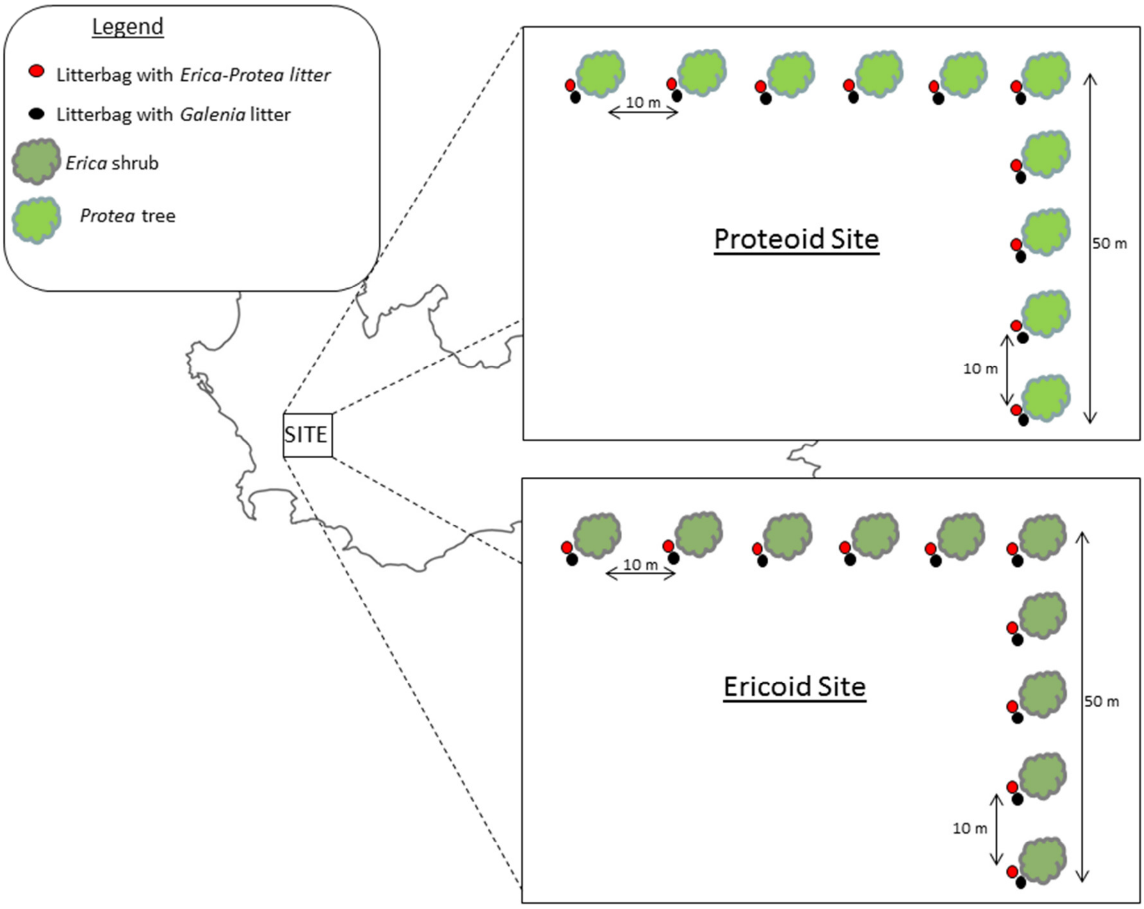


Fig. 7: An illustration of the study design.

Chapter 8

Conclusions

"*All that we have yet discovered is but a trifle in comparison with what lies hid in the great treasury of nature*". – Antonie van Leewenhoek (1680)

The documentation of baseline biodiversity information is essential to enable monitoring in a changing world. Species are lost at an accelerating rate (Magurran & McGill 2011), and we risk losing species to extinction even before they have been documented. This is especially true for invertebrates (Samways et al. 2010). As the need for biodiversity studies increases, the acquisition of taxonomic skills is declining. Despite their significance in soil ecosystems and their use for investigations of soil ecosystem functioning and as bio-indicators elsewhere (Hopkin 1997), springtails (Collembola) have not been well investigated in South Africa (Janion et al. 2011). This may be partly due to a lack of taxonomic knowledge, but also because it has been assumed that the Fynbos biome is generally poor in invertebrate species when compared to other biomes (Giliomee 2003). However, several studies on insects have shown otherwise (Picker & Samways 1996, Botes et al. 2006, Procheş & Cowling 2006, Procheş et al. 2009, Pryke & Samways 2008, 2010).

This thesis represents the first study to investigate the taxonomic and molecular diversity of Collembola in the Fynbos biome, and indeed for any continental area in South Africa. Using detailed sampling in combination with taxonomic expertise and DNA barcoding, this study has revealed a previously undocumented diversity in South Africa. Not only has this project increased the taxonomic knowledge of Collembola in South Africa, but it has also made a contribution to the global Collembola phylogenetic tree with the barcoding approach and association with the BOLD project (Chapter 2). More than 100 species can be considered as new records for the Western Cape, increasing the total known species for this region to 213 species. Many additional Molecular Taxonomic Units (MOTUs) were found through DNA barcoding and may represent several cryptic species, although these will have to be verified using morphological characters and possibly using nuclear genes such as 28S. A start was already made to describe new species to science (see Chapter 3-5, Potapov et al. 2011) and further descriptions are underway.

In addition to taxonomic investigations based on morphological and DNA barcoding, another part of this thesis assessed the diversity of Collembola using quantitative sampling.

Using a temporally replicated litterbag experiment, local species richness was quantified before and after a fire in Jonkershoek Nature Reserve. Although fire is a natural form of disturbance in the fynbos, the frequency of fires is increasing, mainly due to an increase in human population (van Wilgen 2009). In this study it was found that Collembola populations are resilient to fire, recovering after about two years (Chapter 6). These results support recent suggestions that the role of biological decomposition may have been underestimated (Bengtsson et al. 2011, 2012). Furthermore, using litterbag sampling over a wider sampling area, this study showed that the high beta diversity for Collembola is mainly due to species turnover (Chapter 7). Thus, the conservation of this biodiversity hotspot is essential as they contain many localised endemics and undiscovered species.

Possible caveats of the litterbag method include the following: (1) This method does not collect more specialised deeper soil dwelling specimens, (2) an unknown number of individuals might be consumed by predators, (3) some species may reproduce in the litterbag, (4) if the litterbags get flooded with soil, some animals may be trapped in the litterbag and will not be extracted. Despite these caveats, litterbags are a standard and appropriate method to sample soil fauna, and have proven to be extremely efficient during a pilot trial. Also, the mesh size chosen ensured that all sizes of Collembola can be sampled, as this is the group that was focused on.

In conclusion, the information from this study will provide a better understanding of soil biodiversity in the Fynbos biome, which forms an integral and often overlooked part of the ecosystem. In addition, due to our poor knowledge of Collembola in other parts of South Africa, comparisons with other biomes will only be possible once sampling has been extended to other provinces in South Africa. Such work is currently underway. Adopting a multidisciplinary approach in soil research will aid in our growing knowledge of one of the most important but often overlooked components of our world: soil.

Future work should consider the following:

- The potential radiations found for *Seira*, *Ectonura*, *Parisotoma* and *Cryptopygus* should be investigated in more detail in the CFR (Chapter 2). Some of these patterns likely mirror, though unevenly, patterns found in the flora of the region (Linder 2003).

- The role of Collembola as indicators of ecosystem health should be explored. Here endemic species may be especially useful. This will be important with an expected increase in land use change and the need for restoration of native vegetation. For example, over the next 20 years introduced *Pinus radiata* plantations will be removed in Tokai (Liu et al. 2012), while many other disturbed vegetation sites are being rehabilitated.. Nonetheless, the expectation exists that pines and other invasive species will continue to dominate the landscape despite control operations (van Wilgen 2009).
- The impact of introduced collembolan species on the native fauna should be considered as they have been found to occur in large numbers in several sites, even in protected areas investigated (Chapter 7). Studies elsewhere have shown that invasive Collembola species can have a negative impact on the native fauna (Terauds et al. 2011). Experimental studies and quantitative can be useful here, as has been done on sub-Antarctic Marion and Macquarie Island (e.g. Chown et al. 2007, Terauds et al. 2011).
- Lastly, attention should be given to the interactions between above and below ground communities to understand the role of Collembola in ecosystem functioning and their response to global change (see Wardle et al. 2004, Bardgett & Wardle 2010). The prognosis for climate change in the Western Cape is increasing temperatures and locally changing water availability (increasing rainfall in catchments, declines in lowland areas) (Knoesen et al. 2009). Given the sensitivity of springtails to temperature and water availability (Hopkin 1997), substantial impacts might be expected on the group.

In future, analyses of the diversity of springtails at various spatial scales, as is done elsewhere should be possible for South Africa. For example, elsewhere, faunas are well enough known for analyses of small scale variation (Coulson et al. 2000, Hugo et al. 2004), habitat-related variation (Petersen & Luxton 1982, Gabriel et al. 2001), and across major climate gradients (Ulrich & Fiera 2009). However, in South Africa, the information is simply not yet available. Indeed, this was the point of the current thesis and explains much of its form and genesis. Originally, the idea was to examine habitat-related and broad-scale variation in diversity to compare with patterns in plants (e.g. Cowling et al. 1996, Kreft & Jetz 2007), insects (Botes et al. 2006, Procheş & Cowling 2006, Pryke & Samways 2008, Procheş et al. 2009, Pryke & Samways 2010, Brachler et al. 2012, Colville et al. 2002), and other taxa such as birds (van Rensburg et al. 2002). However, it immediately became apparent that taxonomic knowledge of springtails of the Cape Floristic Region, let alone South Africa, is inadequate (Chapter 2). Hence, the study had to commence with training in springtail taxonomy and modern barcoding approaches, listing and revision of the faunal information, and species descriptions (Chapters 2-5). Only thereafter could some idea of the variation in diversity be gained (Chapters 6-7) and as readers will notice, even here key information remains problematic. For example, no comparative assessments of endemism in the Cape Floristic Region compared with others can be made. Indeed, even well-known animal and invertebrate groups knowledge of species richness is far from complete (Essl et al. 2013). The ideal would be for this thesis to spark further work in the area. However, in South Africa, support for soil biology and systematics seems an incomprehensibly low priority by comparison with more esoteric projects such as astronomy. While the universe is likely to continue along its current trajectory for some time, the rate of loss of diversity (e.g. Chown 2010) means that much of it will have vanished before we come to know it, or its significance for our future wellbeing. Thus, although there is evidence that there are more taxonomists than ever before, extinction rates are poorly quantified (Costello et al. 2013). Soils underlie much of our biodiversity patterns (Linder 2003), and support agriculture in the country (Barnard & du Preez 2004), and in so doing contribute to our current and future wellbeing in a major way. Funding priorities for soil health need to be addressed not only for food sustainability and human wellbeing, but also to prevent further extinctions of undiscovered species.

References

Bardgett, R.D. & Wardle, D.A. (2010) Aboveground-belowground linkages. *Biotic Interactions, Ecosystem Processes and Global Change*. Oxford University Press, Oxford.

Barnard, R.O. & du Preez, CC. (2004) Soil fertility in South Africa: the last twenty five years. *South African Journal of Plant and Soil* **21**, 301-315.

Bengtsson, J., Janion, C., Chown, S.L. & Leinaas, H.P. (2011) Variation in decomposition rates in the fynbos biome, South Africa: the role of plant species and plant stoichiometry. *Oecologia* **165**, 225-235.

Bengtsson, J., Janion, C., Chown, S.L. & Leinaas, H.P. (2012) Litter decomposition in the fynbos vegetation, South Africa. *Soil Biology & Biochemistry* **47**, 100-105.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P. & Chown, S.L. (2006) Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**, 71-90.

Braschler, B., Gaston, K.J. & Chown, S.L. (2012) The Fynbos and Succulent Karoo biomes do not have exceptional local ant richness. *PloSONE* **7**, e31463.

Chown, S.L. (2010) Temporal biodiversity change in transformed landscapes: a southern African perspective. *Philosophical Transactions of the Royal Society B* **365**, 3729-3742.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2661-2667.

Colville, J. Picker, M.D. & Cowling R.M. (2002) Species turnover of monkey beetles (Scarabaeidae: Hopliini) along environmental and disturbance gradients in the Namaqualand region of the succulent Karoo, South Africa. *Biodiversity & Conservation* **11**, 243-264.

Costello, M.J., May, R.M. & Stork, N.E. (2013) Can we name Earth's species before they go extinct? *Science* **339**, 413-416.

Coulson, S., Leinaas, H.P., Ims, R.A. & Søvik, G. (2000) Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. *Ecography* **23**, 299-306.

Cowling, R.M., MacDonald, I.A.W. & Simmons, M.T. (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation* **5**, 527-550.

Essl, F., Rabitsch, W., Dullinger, S., Moser, D. & Milasowsky, N. (2013) How well do we know species richness in a well-known continent? Temporal patterns of endemic and widespread species descriptions in the European fauna. *Global Ecology and Biogeography* **22**, 29-39.

Gabriel A.G.A., Chown S.L., Barendse J., Marshall D.J., Mercer R.D., Pugh P.J.A. & Smith V.R. (2001) Biological invasions on Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Giliomee, J.H. (2003) Insect diversity in the Cape Floristic Region. *African Journal of Ecology* **41**, 237-244.

Hopkin, S. (1997) *Biology of the Springtails. Insecta: Collembola*. Oxford University Press, Oxford.

Hugo, E.A., McGeoch, M.A., Marshall, D.J. & Chown, S.L. (2004) Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* **27**, 466-473.

Janion, C., Bedos, A, Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, Liu, A., Malmström, A., Porco, D. & Chown, S.L. (2011a) Springtail diversity in South Africa. *South African Journal of Science* **107**, Art. #582, 7 pages.

Kreft, H. & Jetz, W. (2007) Global Patterns and Determinants of Vascular Plant Diversity. *Proceedings of the National Academy of Sciences of the Unites States of America* **104**, 5925–5930.

Knoesen, D., Schulze, R., Pringle, C., Summerton, M., Dickens, C. & Kunz, R. (2009) Water for the future: impacts of climate change on water resources in the Orange-Senqu River basin. Report to NeWater, a project funded under the Sixth Research Framework of the European Union. Institute of Natural Resources, Pietermaritzburg, South Africa.

Linder, H.P. (2003) The radiation of the Cape flora, southern Africa. *Biological Reviews* **78**, 597-638.

Liu, A., Janion, C. and Chown, S.L. (2012) Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations. *Pedobiologia* **55**, 203-209.

Magurran, A.G. & McGill, B.J. (2011) Challenges and opportunities in the measurement and assessment of biological diversity. In: *Measuring Biological Diversity. Frontiers in Measurement and Assessment*. A.G. Magurran & B.J. McGill (Eds). Oxford University Press, Oxford, pp. 1-7.

Petersen, H. & Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* **39**, 287-388.

Picker, M.D & Samways, M.J. (1996) Faunal diversity and endemicity of the Cape Peninsula, South Africa- a first assessment. *Biodiversity and Conservation* **5**, 591-606.

Potapov, M., Janion, C. & Deharveng, L. (2011) Two new species of *Parisotoma* (Collembola: Isotomidae) from the Western Cape, South Africa. *Zootaxa* **2771**, 17-24.

Procheş, S. & Cowling, R.M. (2006) Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecology and Biogeography* **15**, 445-451.

Procheş, S., Forest, F., Veldtman, R, Chown, S.L., Cowling, R.M., Johnson, S.D., Richardson, D.M. & Savolainen, V. (2009) Dissecting the plant-insect diversity relationship in the Cape. *Molecular Phylogenetics and Evolution* **51**, 94-99.

Pryke, J.S. & Samways, M.J. (2008) Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation* **17**, 3027-3043.

Pryke, J.S. & Samways, M.J. (2010) Significant variables for the conservation of mountain invertebrates. *Journal of Insect Conservation* **14**, 247-256.

Samways, M.J., McGeoch, M.A & New, T.R. (2010) *Insect Conservation. A Handbook of Approaches and Methods.* Oxford University Press, Oxford.

Terauds, A., Chown, S.L. & Bergstrom, D.M. (2011) Spatial scale and species identity influence the indigenous-alien diversity relationship in springtails. *Ecology* **92**, 1436-1447.

Ulrich, W. & Fiera, C. (2009) Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologia* **35**, 45-52.

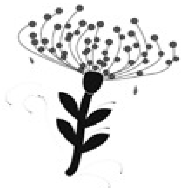
van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist* **159**, 566-577.

van Wilgen, B.W. (2009) The evolution of fire and invasive alien plant management practices in fynbos. *South African Journal of Science* **105**, 335-342.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629-1633.

Appendices

The following list of appendices detail work done over this course of the thesis. However, the work was either led by a different author or not considered part of the current thesis. Nevertheless, it indicates additional academic endeavour in this field over the course of the thesis duration. The appendices are for the reader's interest, and do not form part of the thesis adjudication process.



Springtail diversity in South Africa

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Despite their significance in soil ecosystems and their use for investigations of soil ecosystem functioning and in bioindication elsewhere, springtails (Collembola) have not been well investigated in South Africa. Early recognition of their role in soil systems and sporadic systematic work has essentially characterised knowledge of the southern African fauna for some time. The situation is now changing as a consequence of systematic and ecological work on springtails. To date this research has focused mostly on the Cape Floristic Region and has revealed a much more diverse springtail fauna than previously known (136 identifiable species and an estimated 300 species for the Cape Floristic Region in total), including radiations in genera such as the isotomid *Cryptopygus*. Quantitative ecological work has shown that alpha diversity can be estimated readily and that the group may be useful for demonstrating land use impacts on soil biodiversity. Moreover, this ecological work has revealed that some disturbed sites, such as those dominated by *Galenia africana*, may be dominated by invasive springtail species. Investigation of the soil fauna involved in decomposition in Renosterveld and Fynbos has also revealed that biological decomposition has likely been underestimated in these vegetation types, and that the role of fire as the presumed predominant source of nutrient return to the soil may have to be re-examined. Ongoing research on the springtails will provide the information necessary for understanding and conserving soils: one of southern Africa's major natural assets.

Introduction

The significance of soil organisms for ecosystem functioning and ecosystem service delivery is widely appreciated.[1,2] Amongst the many arthropod taxa that contribute to soil ecosystem functioning, the springtails (Collembola) have been identified as an important group. These small arthropods occur in most ecosystems and may reach densities of several hundred thousand individuals per square metre.[3] They form the prey of a wide variety of soil organisms and ground-living arthropods, actively contribute to soil formation and structure,[4] and have major effects on both plants and plant consumers; and thus link the above-ground and below-ground components of terrestrial systems.[2,5] The ecological roles and abundance of springtails in terrestrial systems have also led to their recognition as important organisms for bioindication,[6,7] and as model organisms in ecotoxicology.[8] Consequently, springtails have been the subject of substantial and long-standing interest, especially in Europe and North America.[3,9,10]

The significance of springtails in soil systems in South Africa is unlikely to be different from that elsewhere, recognising that springtails reach their highest species richness and abundance in moist habitats rather than in arid areas.[11,12] However, in contrast with many other regions of the world,[10] and with other components of the soil fauna in South Africa, such as the ants,[13,14,15,16] springtails have, until recently, been the subject of little attention. Early research recognised that springtails are likely to play an important role in various South African biomes,[17] and since the initial work of Womersley[18], ongoing, but sporadic and typically restricted taxonomic investigations have been made.[19,20,21,22,23,24,25,26,27,28] Few investigations have sought to understand comprehensively the diversity of the group (at present the only available, but unpublished list by P. Greenslade, places the fauna at about 43 genera and 90 species for the Western Cape), their contribution to ecosystem functioning, and their utility for bioindication,[29] although occasional attempts at doing so have been made.[30] The exception is research on the group undertaken in the sub-Antarctic Tundra and Polar Desert biomes of the Prince Edward Islands, which, at least geopolitically, form part of South Africa.[31] For these island biomes, the limited fauna of 16 species is relatively well understood.[32,33,34,35,36] Perhaps more significantly, it is this island work that has precipitated a recent and substantial change in current understanding of springtail ecology and systematics in continental South Africa.

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On the basis of a comprehensive comparison of the likely effects of climate change on indigenous versus invasive springtails on the Prince Edward Islands, funded by a bilateral grant under the South Africa–Norway agreement (Table 1),[34] a second project was developed to compare life histories of species in polar systems (namely, the Prince Edward Islands and Svalbard, Norway) and more temperate systems (southern Norway and the Western Cape Province, South Africa). This work sought also to investigate the implications thereof for ecosystem functioning and drew in further expertise from Sweden and support from a South Africa–Sweden bilateral (Table 1). In both cases, it was recognised from the outset that the springtails in South Africa are poorly known systematically, and that this taxonomic impediment[37] would therefore constrain work substantially. Thus, additional collaborations were established with systematic experts under a third bilateral agreement (South Africa–France) and with the support of the International Barcode of Life project (iBOL - http://ibol.org) (Table 1). Here we report on research so far undertaken across these major projects, how systematic and ecological understanding of the group is progressing for South Africa, and the prospects for ongoing research and future collaborations amongst researchers with an interest in soil diversity and ecosystem functioning.

Systematics and barcoding

Owing to estimates of the likely large size of the South African springtail fauna, the collaborative research was established to investigate the diversity of the Cape Floristic Region, focusing mostly on fynbos, renosterveld and forest vegetation. From the outset, the research approach emphasised collection across a range of sites in a systematic fashion (Figure 1) for estimates of richness and abundance, supplemented by *ad hoc* collections from as wide a range of habitats as possible for the systematic and barcoding studies. Importantly, our investigations combined traditional taxonomy and barcoding to ensure an integrated, modern approach to the systematics of the group.

Initial assessments of the published taxonomic research indicated a faunal assortment of 90 species in 16 families, but, excluding incorrect identifications, only 57 valid and recognisable species (Table 2a). Now, based on a geographically extensive collection of more than 450 samples from the Western Cape (Figure 1), it is clear that the faunal component is much larger. The collection methods included high gradient extraction of litter bags; Berlese–Tullgren extraction of leaf litter, moss and rotten wood; vegetation beating and collection by hand (especially in caves and streams); pitfall trapping; litter sifting; and soil washing (of beach and deep soil sand). The current faunal assemblage stands at 136 morphospecies in 19 families (Table 2b), but only half of the samples have been sorted to species so far and not all microhabitats have been surveyed to completion. Moreover, assessments of previous lists (in particular Paclt[19]) for the country, the examination of museum specimens and barcoding work have indicated that many species have been misidentified and that several groups have either cryptic species or have shown substantial radiations. For example, more than 11 *Cryptopygus* and 7 *Parisotoma* species were found during our survey, in contrast to only 2 species that have been previously recorded – *Cryptopygus caecus* and *Parisotoma notabilis*.[19] In addition, 23 described species of *Seira* are found in South Africa,[22] whilst only 1 species is described from Australia.[38] These groups that have radiated in the Cape Floristic Region are now the subject of closer investigation from the classical taxonomic[39,40] and barcoding perspectives. Thus, although research to date has more than doubled the number of known species, based on our experience from elsewhere it seems likely that at least 300 species will be characteristic of the regional (i.e. Cape Floristic Region) fauna. For South Africa as a whole the richness is certainly much higher. Even so, the Collembola likely has fewer species

TABLE 1: A summary of the springtail research undertaken over the past decade in South Africa, funded mostly through bilateral research agreements. In each case the partner country, project title, areas of work and outputs (e.g. numbers of students advised, investigators involved and papers published) are indicated. The International Barcode of Life (iBOL)-related work is not listed as a separate project because it was initiated within the South Africa–France bilateral agreement. This work is now being pursued both through another project within the same bilateral agreement and through support from a larger, barcoding initiative established with funding from iBOL and managed by the South African Institute for Aquatic Biodiversity.

Partner country	Duration	Project title	Research areas	Location	Outputs
France	2009–2010	Uncovering springtail diversity in the South African Cape Floristic Region: A combined taxonomic and barcoding approach	Systematics, barcoding, invasion biology and quantitative biodiversity assessments	France and the Western Cape Province, South Africa	Two students, four investigators, two research papers, three presentations and two media interactions; 504 springtail specimens barcoded to date
France	2011/12 on	Springtail diversity in the Western Cape: The combined result of multiple radiations, high endemism and strong ties with Europe	Systematics, barcoding, invasion biology and quantitative biodiversity assessments	France and the Western Cape Province, South Africa	Two students and three investigators; project recently commenced
Norway	2004–2006	Environmental responses of springtails: Implications for climate change	Life histories, physiology, ecology and invasion biology	Norway, Marion Island and Svalbard	Seven students, two investigators, five research papers, six presentations and four media interactions
Norway	2007–2010	Springtail responses to changing and variable environments: A bipolar approach linking individuals to ecosystems	Distribution and abundance, life histories, physiology and ecosystem functioning	Norway, Marion Island, Svalbard and the Western Cape Province, South Africa	Three students, two investigators, six research papers, seven presentations and two media interactions
Sweden	2007–2010	Soil biodiversity in the fynbos: Patterns and processes	Soil biology, soil biochemistry, nutrient release, ecosystem functioning, systematics and abundance and distribution	Sweden and the Western Cape Province, South Africa	Five students, five investigators, three research papers and two media interactions

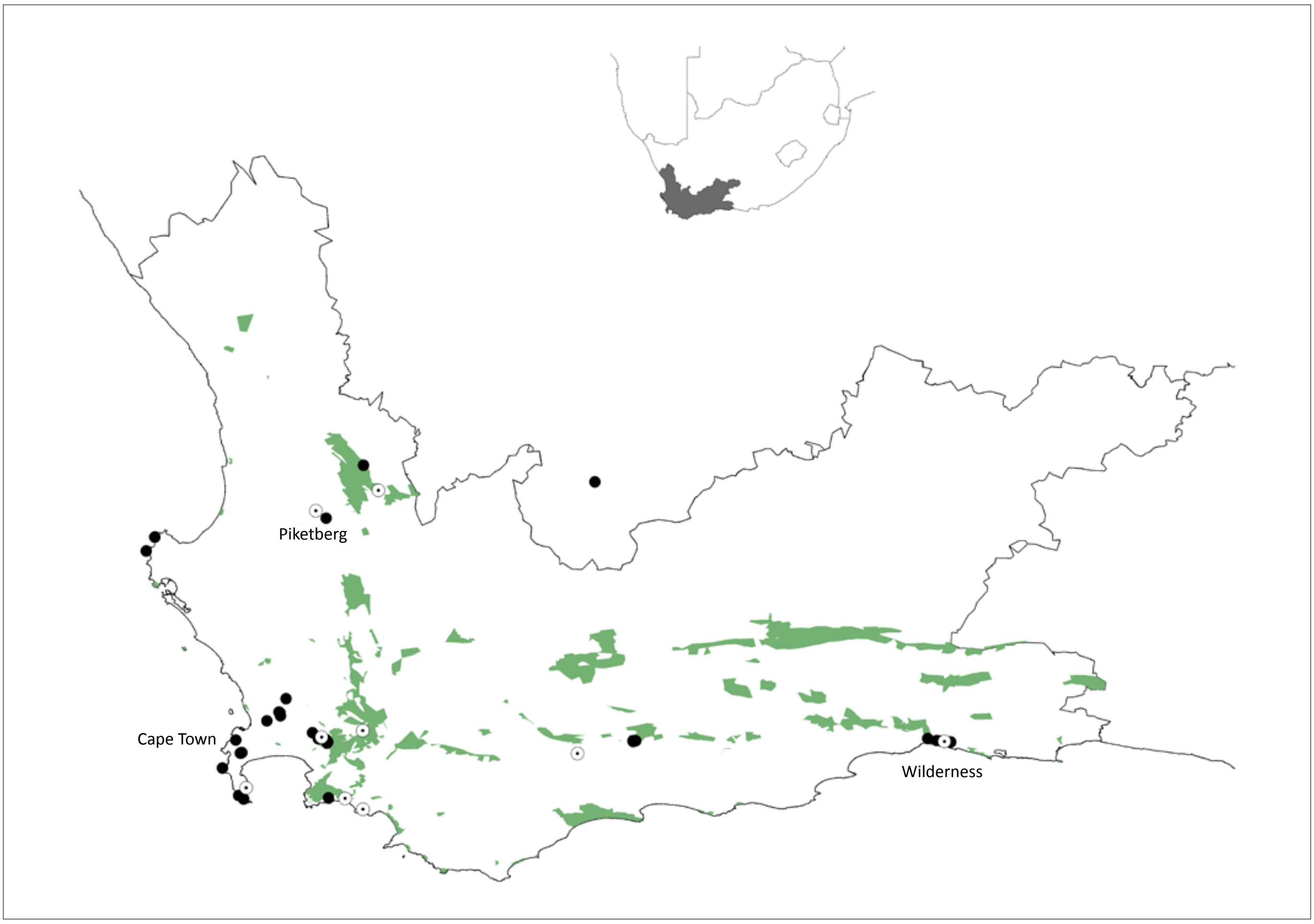


FIGURE 1: Systematic (⊙) and *ad hoc* (●) sampling sites for the current springtail diversity assessments in the Western Cape Province, South Africa. Protected areas are overlaid in shading.

than are found in the highly diverse insect orders, such as the Coleoptera or Lepidoptera.[41] Many sequences obtained from barcoding have been connected to traditional taxonomic species, although certain species with poor morphological descriptions have been more difficult (as in the case of several *Seira* species). The barcoding results have also led to careful re-examination of the individuals traditionally assigned to the widespread species *Parisotoma notabilis*, which actually represent a group of several similar species of endemic *Parisotoma*. In addition, the barcoding has proven not only to be of particular importance to detect introduced species of complex groups (e.g. *Isotomurus maculatus*), but also to show that some forms expected to be European actually do not match any European cluster (such as one cluster of *Isotomurus* and several of *Ceratophysella*).

Invasions and diversity estimation

Amongst the 136 species-level taxa identified for the Western Cape, at least 34 represent species either with wide distributions or known or suspected to have been introduced from elsewhere. Based on our preliminary molecular analysis, two of these species – *Neanura muscorum* and *Isotomurus cf. maculatus* – have already been shown to be invasive, occurring locally in fynbos or forest habitat. Similar comparisons between South African and European populations of other suspected invasive species are in progress. For example, in an investigation of diversity and decomposition rates in renosterveld fragments in the Piketberg area,[42] the springtail assemblages were dominated (60% by abundance) by a single species, *Hypogastrura manubrialis*, which is widely distributed in Europe,[43] and clearly is an invasive species in the Western Cape. Similarly, two *Isotomurus* species, thought to be introduced to the region, were also found in high abundance in a preliminary assessment of the diversity of springtails in Cape Flats Sand Fynbos and an adjacent pine plantation in the Tokai Forest Reserve, which forms part of Table Mountain National Park; these species were restricted to the pine plantation. This study also showed that springtail abundance and species richness (but not species identity) differ significantly amongst these two major habitat types, and, that for complete estimation of the fauna using a litter sampling technique (for each sample: 1 L of litter collected over a standardised 1 m^2 and then extracted by a Berlese–Tullgren funnel in the laboratory), the extent of sampling is not so onerous that it precludes reasonably straightforward estimation of local (alpha) diversity (Figure 2). In consequence, the springtails could be used for assessments of soil health, as they are elsewhere.[3,9]

Ecosystem functioning

In the context of soil health, the influence of springtails on litter decomposition rates and nutrient cycling, including

TABLE 2a: Number of springtail species in the Western Cape Province, South Africa in each of the springtail families as listed in the systematic literature as of November 2010.

Order	Family	From the literature				
		Genera	Species	Species identifications incorrect	Identification probably correct	Introduced or widely distributed
Entomobryomorpha	Cyphoderidae	1	4	1	3	0
	Entomobryidae	5	31	14	17	4
	Paronellidae	0	0	0	0	0
	Isotomidae	6	10	3	7	5
	Tomoceridae	1	1	0	1	0
	Oncopoduridae	0	0	0	0	0
	Total	13	46	18	28	9
Neelipleona	Neelidae	1	1	0	1	1
	Total	1	1	0	1	1
Poduromorpha	Brachystomellidae	3	6	2	4	1[a]
	Hypogastruridae	4	10	5	5	3
	Neanuridae	5	5	0	5	1
	Odontellidae	1	1	0	1	0
	Onychiuridae	3	3	2	1	0
	Tullbergiidae	3	3	1	1	1
	Total	19	28	10	17	5
Symphypleona	Bourletiellidae	4	6	1	5	1
	Dicyrtomidae	1	2	0	2	1
	Katiannidae	3	5	2	3	0
	Sminthuridae	1	1	0	1	1
	Sminthurididae	1	1	1	0	0
	Total	10	15	4	11	3
TOTAL		**43**	**90**	**32**	**57**	**18**

[a], Exact status of species unknown.

TABLE 2b: Number of springtail species in the Western Cape Province, South Africa added from our own collections (as of November 2010).

Order	Family	Additions from our collections			Total (including those reported from the literature)	
		Genera	Species or morpho-species	Introduced or widely distributed	Genera	Species
Entomobryomorpha	Cyphoderidae	0	0	0	1	3
	Entomobryidae	3	11	1	8	28
	Paronellidae	1	1	0	1	1
	Isotomidae	9	28	7	15	35
	Tomoceridae	1	1	1	2	2
	Oncopoduridae	1	1	0	1	1
	Total	15	42	9	28	70
Neelipleona	Neelidae	1	1	1	2	2
	Total	1	1	1	2	2
Poduromorpha	Brachystomellidae	0	1	0	3	5
	Hypogastruridae	2	5	2	6	10
	Neanuridae	5	12	1	10	17
	Odontellidae	1	2	0	2	3
	Onychiuridae	1	1	1	4	2
	Tullbergiidae	3	8	3	6	9
	Total	12	29	7	31	46
Symphypleona	Bourletiellidae	0	0	0	4	5
	Dicyrtomidae	0	0	0	1	2
	Katiannidae	0	3	0	3	6
	Mackenziellidae	1	1	0	1	1
	Sminthuridae	1	2	0	2	3
	Sminthurididae	1	1	0	2	1
	Total	2	6	0	12	17
TOTAL		**31**	**79**	**17**	**74**	**136**

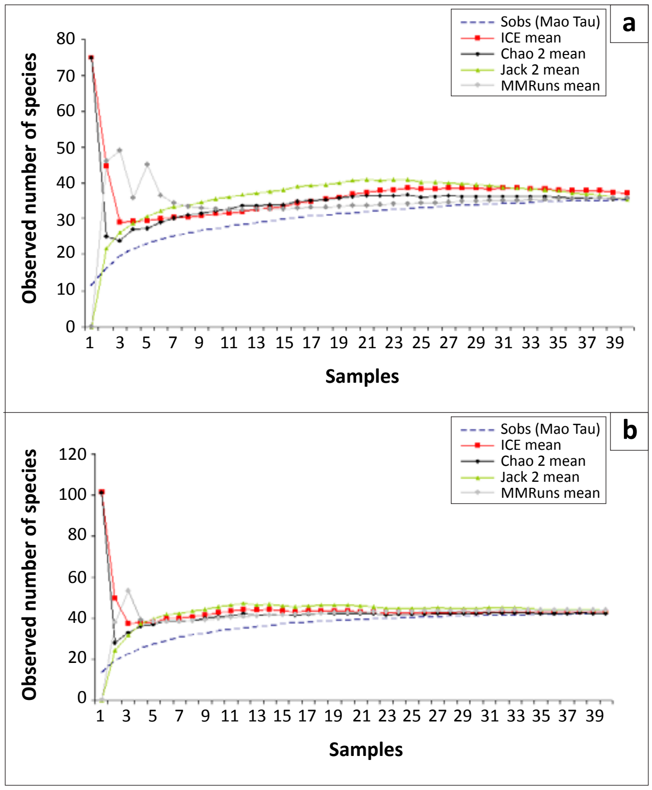
the ways in which litter type, spatial position and home-field advantage influence decomposition, has long been of interest to soil ecologists.[45,46,47,48,49] As a consequence of the research priorities identified within our South Africa–Sweden and South Africa–Norway bilateral projects (Table 1), we have also been concerned with these questions. The dominant paradigm for the Fynbos biome has been that loss of organic matter and nutrient cycling take place largely as a consequence of fires, which, with an average fire frequency of 11 years,[50] return nutrients accumulated in litter to the soil. Biological decomposition was largely relegated to a less significant role.[51,52,53]

During the investigation of springtail diversity in renosterveld fragments, decomposition of the litter of three representative plant species was also investigated. Decomposition of these species varied between 0.00674/day for *Galenia africana*, a shrub favoured by disturbances such as overgrazing, to 0.00222/day for renosterbos *Elytropappus rhinocerotis* and 0.00029/day for the sturdy geophyte *Watsonia borbonica*, corresponding to litter half-lives of 0.3, 0.8 and 6 years, respectively.[42] The rates for *Galenia* and renosterbos are much faster than those previously found for litter of the fynbos species *Leucadendron parile* and *Protea repens*.[51,52] However, they are not unusual compared with other fynbos species we have studied (Figure 3; personal observation).

If the mean fire return time for fynbos systems is about 11 years,[50] and if decomposition of the less hardy species proceeds such that many litters have half-lives that are less than half this time, then biological decomposition as a nutrient recycling process is much more significant than previously estimated.[53] Ultimately, the significance of this decomposition will depend on the relative contributions of species with more readily or less readily decomposed litter to the litter pool of any given system. To date, such estimates have not been made. Species with high decomposition rates of the kinds we investigated clearly make a significant contribution to the fynbos flora, and it is obvious that litter of many species do not accumulate on the ground in the way that some *Protea* species do (personal observations). Thus, the current research on ecosystem functioning has demonstrated that important as fire is in the Fynbos biome, it may be complemented and sometimes surpassed by other processes.

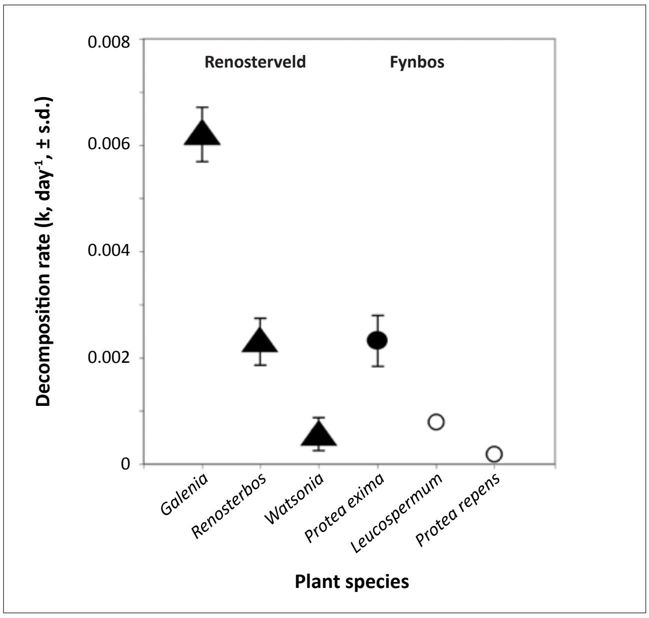
Conclusions

Our research on springtails has thus far revealed not only a hitherto undocumented diversity in South Africa, but also that the group may be much more significant for ecosystem functioning than previously thought. Given a growing human population and its impacts on the environment,[54] national requirements for sustainable development and conservation, and the need to provide measures of conservation and sustainable development success internationally, ongoing work on the Collembola will prove both useful and valuable. The current collaborations described here will continue throughout the duration of the International Barcode of Life initiative (iBOL - http://ibol.org), with support from several institutions, both in South Africa and abroad, and growing interest from various sectors in demonstrating soil health and conservation success. Moreover, as this knowledge



Sobs, observed number of species; ICE, Incidence Coverage Estimator; Chao 2, richness estimator; Jack 2, second-order Jackknife richness estimator; MMRuns, Michaelis-Menten richness estimate.
Each sample was 1 L of litter.
All estimators were calculated using EstimateS V8.2.[44]

FIGURE 2: Sample-based species rarefaction curves for the (a) Cape Flats Sand Fynbos and (b) *Pinus radiata* sites.



k, decomposition constant.
○ indicates earlier studies.[51,52]

FIGURE 3: Decomposition rates per day (mean ± s.d.) of various renosterveld and fynbos species: *Galenia africana*, renosterbos (*Elytropappus rhinocerotis*) and *Watsonia borbonica*[42] (▲); *Protea exima*[53] (●); and *Leucospermum parile* and *Protea repens*[51,52] (○).

develops so more information will be made available through the project home page (www.sun.ac.za/cib/collembola). Our long-term aims are to encourage additional work on the group in the southern African region, and to foster collaborations that can enhance understanding of this significant group of organisms. Underlying these aims is the realisation that sustainable development and conservation must continue to focus on one of southern Africa's major natural assets: the soil.

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Competing interests

We declare that we have no financial or personal relationships which may have inappropriately influenced us in writing this article.

Authors' contributions

S.L.C. was the project leader; A.B., L.D., H.P.L. and C.J. provided taxonomic data; H.P.L., J.B., A.M. and C.J. provided decomposition data; A.L. provided rarefaction curves; and D.P. and B.J.V.V. provided data on barcoding.

References

1. Wardle DA. Communities and ecosystems: Linking the aboveground and belowground components. Princeton, NJ: Princeton University Press; 2002.
2. Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van der Putten WH, Wall DH. Ecological linkages between aboveground and belowground biota. Science. 2004;304:1629–1633. http://dx.doi.org/10.1126/science.1094875, PMid:15192218
3. Hopkin S. Biology of the springtails. Insecta: Collembola. Oxford: Oxford University Press; 1997.
4. Rusek J. Soil microstructures-contributions on specific soil organisms. Quest Ent. 1985;21:497–514.
5. Scheu S, Treenhaus A, Jones TH. Links between the detritivore and the herbivore system: Effects of earthworms and Collembola on plant growth and aphid development. Oecologia. 1999;119:541–551. http://dx.doi.org/10.1007/s004420050817
6. Deharveng L. Soil Collembola diversity, endemism, and reforestation: A case study in the Pyrenees (France). Conserv Biol. 1996;10:74–84. http://dx.doi.org/10.1046/j.1523-1739.1996.10010074.x
7. Cassagne N, Gauquelin T, Bal-Serin M-C, Gers C. Endemic Collembola, privileged bioindicators of forest management. Pedobiologia. 2006;50:127–134. http://dx.doi.org/10.1016/j.pedobi.2005.10.002
8. Van Straalen NM, Van Gestel CAM. Soil invertebrates and microorganisms. In: Calow P, editor. Handbook of ecotoxicology. Oxford: Blackwell; 2009.
9. Rusek J. Biodiversity of Collembola and their functional role in the ecosystem. Biodiv Conserv. 1998;7:1207–1219. http://dx.doi.org/10.1023/A:1008887817883
10. Deharveng L. Recent advances in Collembola systematics. Pedobiologia. 2004;48:415–433. http://dx.doi.org/10.1016/j.pedobi.2004.08.001
11. Petersen H, Luxton M. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos. 1982;39:287–388. http://dx.doi.org/10.2307/3544689
12. Ulrich W, Fiera C. Environmental correlates of species richness of European springtails (Hexapoda: Collembola). Acta Oecol. 2009;35:45–52. http://dx.doi.org/10.1016/j.actao.2008.07.007
13. Robertson HG. Afrotropical ants (Hymenoptera: Formicidae): Taxonomic progress and estimation of species richness. J Hymen Res. 2000;9:74–84.
14. Parr CL, Robertson HG, Biggs HC, Chown SL. Response of African savanna ants to long-term fire regimes. J Appl Ecol. 2004;41:630–642. http://dx.doi.org/10.1111/j.0021-8901.2004.00920.x
15. Botes A, McGeoch MA, Robertson HG, Van Niekerk A, Davids HP, Chown SL. Ants, altitude and change in the northern Cape Floristic Region. J Biogeogr. 2006;33:71–90. http://dx.doi.org/10.1111/j.1365-2699.2005.01336.x
16. Braschler B, Kirsten M, Karenyi N, Gaston KJ, Chown SL. Realizing a synergy between research and education: How participation in ant monitoring helps raise biodiversity awareness in a resource-poor country. J Insect Cons. 2010;14:19–30. http://dx.doi.org/10.1007/s10841-009-9221-6
17. Lawrence RF. The biology of the cryptic fauna of forests, with special reference to the indigenous forests of South Africa. Cape Town: Balkema; 1953.
18. Womersley H. On some Collembola Arthropleona from South Africa and southern Rhodesia. Ann S Afr Mus. 1934;30:441–475.
19. Paclt J. Collembola. In: Hanstrom B, Brinck P, Rudebeck G, editors. South African animal life. Results of the Lund University Expedition in 1950–1951. Vol. VI. Uppsala: Almqvist & Wiksells Boktryckeri AB, 1959; p. 24–78.
20. Yosii R. Collembola fauna of the Cape Province, with special reference to the genus *Seira* Lubbock. In: Biological results of the Japanese Antarctic Research Expedition 6. Kyoto: Siraham, Wakayam-Ken, 1959; p. 1–23.
21. Coates TJ. The Collembola of South Africa – 1: The genus *Neanura*. J Ent Soc Sth Afr. 1968;31:185–195.
22. Coates TJ. The Collembola of South Africa – 2: The genus *Seira*. J Ent Soc Sth Afr. 1968;31:435–462.
23. Coates TJ. The Collembola of South Africa – 3: The genus *Lepidokrugeria*. J Ent Soc Sth Afr. 1969;32:87–89.
24. Coates TJ. Check-list of the Collembola of South African Parks (Part 1). Koedoe. 1970;13:181–184.
25. Weiner WM, Najt J. Collembola Poduromorpha of South Africa. Bonn Zool Beitr. 1991;42:369–387.
26. Barra J-A. Nouveaux Collemboles Poduromorphes de la Province du Natal (Rép. Sud Africaine) (Insecta: Collembola). [New Poduromorpha Collembola from Natal Province (Republic of South Africa) (Insecta: Collembola)]. J Afr Zool. 1994;108:181–189. French.
27. Barra J-A. Nouveaux Collemboles Poduromorphes des sables littoraux (partie terrestre) de la Province du Natal (Rép. Sud Africaine) (Insecta : Collembola). [New Poduromorpha Collembola from the sand coasts (terrestrial part) from Natal Province (Republic of South Africa) (Insecta: Collembola)]. J Afr Zool. 1995;109:125–139. French.
28. Barra J-A. Nouveaux Collemboles Entomobryomorphes des sables littoraux (partie terrestre) de la Province du Natal (Rép. Sud Africaine) (Insecta : Collembola). [New Entomobryomorpha Collembola from the sand coasts (terrestrial part) of the Natal Province (Republic of South Africa) (Insecta : Collembola)]. J Afr Zool. 1997;111:465–480. French.
29. McGeoch MA. The selection, testing and application of terrestrial insects as bioindicators. Biol Rev. 1998;73:181–201. http://dx.doi.org/10.1017/S000632319700515X
30. Reinecke AJ, Albertus RMC, Reinecke SA, Larink O. The effects of organic and conventional management practices on feeding activity of soil organisms in vineyards. Afr Zool. 2008;43:66–74. http://dx.doi.org/10.3377/1562-7020(2008)43[66:TEOOAC]2.0.CO;2
31. Chown SL, Froneman PW. The Prince Edward Islands. Land-sea interactions in a changing climate. Stellenbosch: African Sun Media; 2008.
32. Deharveng L. Collemboles des iles subantarctiques de l'Océan Indien Mission J. Travé 1972–1973. [Collembola of the sub-Antarctic islands of the Indian Ocean Mission J. Travé 1972–1973]. Com Nat Fr Rech Antarct. 1981;48:33-108. French.
33. Gabriel AGA, Chown SL, Barendse J, et al. Biological invasions on Southern Ocean islands: The Collembola of Marion Island as a test of generalities. Ecography. 2001;24:421–430. http://dx.doi.org/10.1034/j.1600-0587.2001.d01-198.x
34. Chown SL, Slabber S, McGeoch MA, Janion C, Leinaas HP. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. Proc R Soc Lond B. 2007;274:2661–2667. http://dx.doi.org/10.1098/rspb.2007.0772, PMid:17686728, PMCid:2275886
35. Myburgh M, Chown SL, Daniels SR, Jansen van Vuuren B. Population structure, propagule pressure, and conservation biogeography in the sub-Antarctic: Lessons from indigenous and invasive springtails. Divers Distrib. 2007;13:143–154.
36. Janion C, Leinaas H-P, Terblanche JS, Chown SL. Trait means and reaction norms: The consequences of climate change/invasion interactions at the organism level. Evol Ecol. 2010;24:1365–1380. http://dx.doi.org/10.1007/s10682-010-9405-2
37. Samways MJ. Insect conservation biology. London: Chapman & Hall; 1994.
38. Greenslade P. Collembola. In: Houston VWK, editor. Zoological catalogue of Australia. Volume 22. Protura, Collembola, Diplura. Melbourne: CSIRO, 1994; p. 19–138.
39. Potapov M, Janion C, Deharveng L. Two new species of *Parisotoma* (Collembola: Isotomidae) from the Western Cape, South Africa. Zootaxa. 2011;2771:17–24. PMid:21547000, PMCid:3086760

40. Janion C, Bedos A, Deharveng L. The genus *Ectonura*, Cassagnau 1980 in South Africa (Collembola: Neanuridae: Neanurinae), with a key to South African Neanurinae. ZooKeys. 2011;136:31–45.

41. Scholtz CH, Chown SL. Insects in southern Africa: How many species are there? S Afr J Sci. 1995;91:124–126.

42. Bengtsson J, Janion C, Chown SL, Leinaas HP. Variation in decomposition rates in the fynbos biome, South Africa: The role of plant species and plant stoichiometry. Oecologia. 2011;165:225–235. http://dx.doi.org/10.1007/s00442-010-1753-7, PMid:20827492, PMCid:3015188

43. Fjellberg A. The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha. Fauna Entomologica Scandinavica 35. Leiden: Brill; 1998.

44. Colwell RK. EstimateS: Statistical estimation of species richness and shared species from samples (software and user's guide). Version 8.2.0. Storrs, CT: University of Connecticut; 2009.

45. Seastedt TR. The role of microarthropods in decomposition and mineralization processes. Annu Rev Entomol. 1984;29:25–46.

46. Verhoef H, Brussaard L. Decomposition and nitrogen mineralization in natural and agro-ecosystems: The contribution of soil animals. Biogeochemistry. 1990;11:175–211. http://dx.doi.org/10.1007/BF00004496

47. Barrios E. Soil biota, ecosystem services and land productivity. Ecol Econ. 2007;64:269–285.

48. Ettema CH, Wardle DA. Spatial soil ecology. Trends Ecol Evol. 2002;17:177–183. http://dx.doi.org/10.1016/S0169-5347(02)02496-5

49. Ayres E, Steltzer H, Simmons BL, et al. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biol Biochem. 2009;41:606–610.

50. Van Wilgen BW. The evolution of fire and invasive alien plant management practices in fynbos. S Afr J Sci. 2009;105:335–342.

51. Mitchell DT, Coley PGF, Webb S, Allsopp N. Litter fall and decomposition processes in the coastal fynbos vegetation, south-western Cape, South Africa. J Ecol. 1986;74:977–993.

52. Mitchell DT, Coley PGF. Litter production and decomposition from shrubs of *Protea repens* growing in sand plain lowland and mountain fynbos, south-western Cape. S Afr J Bot. 1987;53:25–31.

53. Stock WD, Allsopp N. Functional perspective of ecosystems. In: Cowling RM, editor. The ecology of fynbos: Nutrients, fire and diversity. Cape Town: Oxford University Press, 1992; p. 241–259.

54. Chown SL. Temporal biodiversity change in transformed landscapes: A southern African perspective. Phil Trans R Soc B. 2010;365:3729–3742.

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Article

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Two new species of *Parisotoma* (Collembola: Isotomidae) from the Western Cape, South Africa

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Abstract

Two new species, *Parisotoma sexsetosa* **sp. nov.** and *P. obscurocellata* **sp. nov.**, are described from the Western Cape Province in South Africa. The former is characterized with 2+2 ocelli and 4 sensilla in the p-row on each side of three first abdominal segments, the latter with 5+5 or more ocelli and 3+3 chaetae on the postlabial area. Both species have only 6 posterior chaetae on dens. A comparison of South African and Asiatic *Parisotoma* species is given. Sensillar chaetotaxy of the third and fourth abdominal segments is critical in the separation of these geographically distinct groups.

Key words: disjunct distribution, diversity, fynbos, sensilla

Introduction

To date, only one species of the genus *Parisotoma* Bagnall, 1940 has been recorded from South Africa, namely *P. notabilis* (Schäffer) (Paclt 1959, 1967). Among Isotomidae described from this country, none belongs to this genus (see Barra 1995, 1997, 2001). However, during recent investigation of the soil fauna in the fynbos of South Africa, it appeared clearly that species of *Parisotoma* tend to dominate in soil arthropod communities, both in number and in diversity. Here, we describe two remarkable new species of this fauna, one from the Table Mountain National Park, and another from the Betty's Bay area.

Abbreviations: Abd.I–VI—abdominal segments; accp-sensillum—p-row accessorial tergal sensillum; Ant.I–IV—antennal segments; AO III—antennal organ of antennal segment III; ms—microsensillum; PAO—postantennal organ; s—sensillum; Th.I–III—thoracic segments.

Material deposit: MNHN—Museum national d'Histoire naturelle of Paris; MSPU—Moscow State Pedagogical University; Iziko Museum, Cape Town (South Africa).

General remarks on *Parisotoma* of South Africa

The genus *Parisotoma* is distributed all over the world, partly due to the cosmopolitan species *P. notabilis* and the Holarctic species *P. ekmani* (Fjellberg). Most other species have more restricted ranges. In the Northern Hemisphere, the largest diversity has been recorded in Northern Asia, with at least 12 species. In contrast, the tropics are practically devoid of *Parisotoma*. Similar number of species have been recorded in both hemispheres illustrating a remarkable disjunct distribution of the genus. However, many of the "southern" species call for re-description, and their generic position is uncertain. That is particularly true for several New Zealand forms. The real diversity of *Parisotoma* will only be fully understood with further studies. This is particularly obvious with the discovery of the rich fauna of South Africa.

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In spite of a spatially limited sampling, our material contained at least seven species that unambiguously belong to the genus *Parisotoma*, following the rather strict diagnosis of the genus given by Deharveng (1981), Rusek (1984), and Potapov (1991). All of these species have pale grey pigmentation, fewer than 8 ocelli (see remarks to *P. obscurocellata* **sp. nov.**), tridentate mucro, few chaetae on appendages and postlabial area, and large oval PAO. Such a rich diversity of South African *Parisotoma* led us to search for morphological differences between northern (North Asia) and southern (South Africa) species of the genus. The most distinctive characters of the South African group that we observed are the mid-tergal position of accp4 sensilla on Abd.IV and the absence of microsensilla on Abd.II (Table 1, Figs 3–6). After its morphological characters, the cosmopolitan species *P. notabilis* formally belongs to the "Northern Asiatic" group. Chaetal reduction, however, may mask this difference. Several Northern Asiatic species lost accp4 sensilla (*P. trichaetosa* (Martynova) and *P. ekmani*), so do *P. sexsetosa* and two undescribed species from South Africa (see Fig. 57 in Potapov (1991) and Fig. 23 in the present paper). In these species, only absence/presence of microsensillum on Abd.II can indicate the species-group to which they belong. Odd species like *P. ekmani* (Holarctic) have also lost ms on Abd.II, resulting in uncertain group position according to current taxonomy. Following Occam´s razor, we accept the homology, i.e. shift of accp4 sensillum when comparing Northern Asiatic and South African specimens. In other characters, South African species show greater variation in posterior chaetotaxy of the dens and lower variation in chaetotaxy of the ventral tube than Northern Asiatic group. Our conclusions can possibly get wider generalization since the Australian species *P. greensladeae* (Rusek, 1984) shows the same position of accp4 as in species from South Africa (according to Fig. 13B in Rusek 1984).

TABLE 1. Characters of "Northern Asiatic" and "South African" groups of *Parisotoma*.

Character	North Asiatic species*	South African species**
Number of laterodistal chaetae on ventral tube	2+2 to 4+4	2+2
Number of posterior chaetae on dens	7–8	6–14
number of accp-sensilla on body tergites	4–6,4–7/3–6,3–6,4–6,5–6,5	4–6,4–6/4–6,4–6,4–6,5–6,5
number of teeth on mucro	3–4	3
position of accp4-sensilla on Abd.IV	in p-row	in mid-tergal position
ms on Abd.II	present (absent in *P. ekmani*)	absent

* *P. amurica* (Potapov), *P. appresopilosa* (Potapov), *P. atroculata* (Potapov), *P. ekmani* (Fjellberg), *P. hyonosenensis* (Yosii), *P. longa* (Potapov), *P. reducta* (Rusek), *P. removeophthalma* (Martynova), *P. terricola* (Rusek), *P. trichaetosa* (Martynova), *P. vtorovi* (Martynova). ** *P. obscurocellata* **sp. nov.**, *P. sexsetosa* **sp. nov.** and 5 undescribed species.

Description of new species

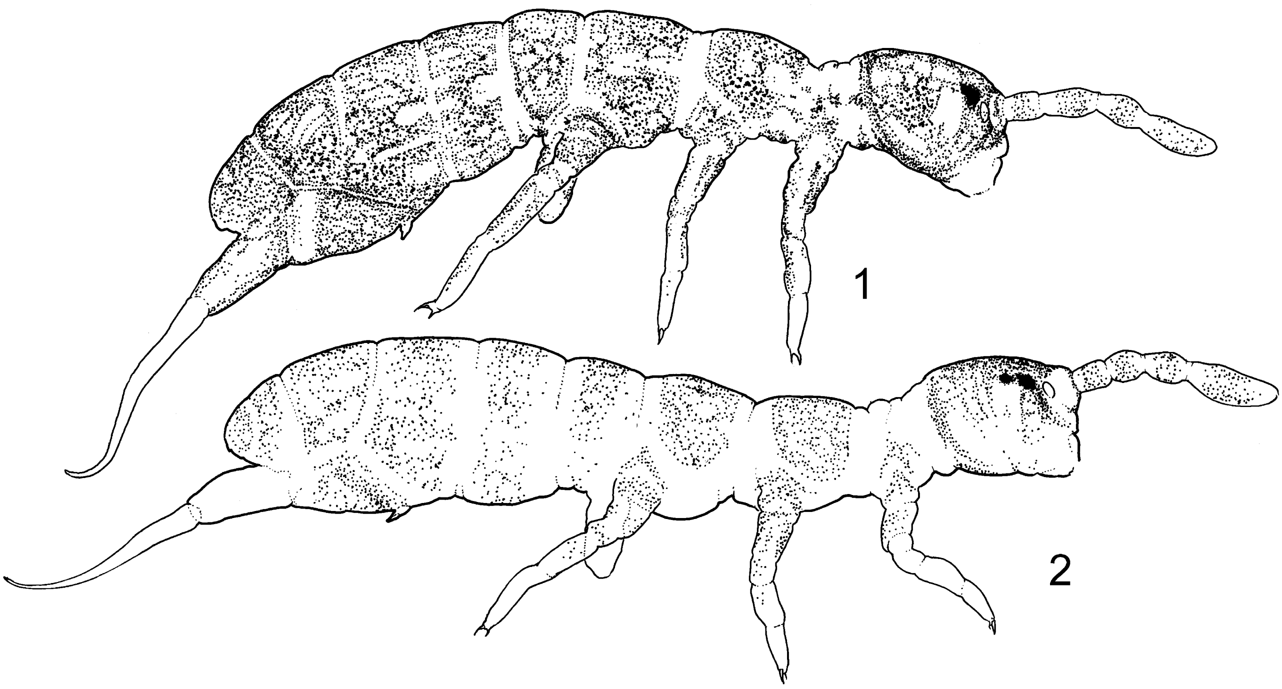
Parisotoma sexsetosa sp. nov.

Figs 1, 7–23.

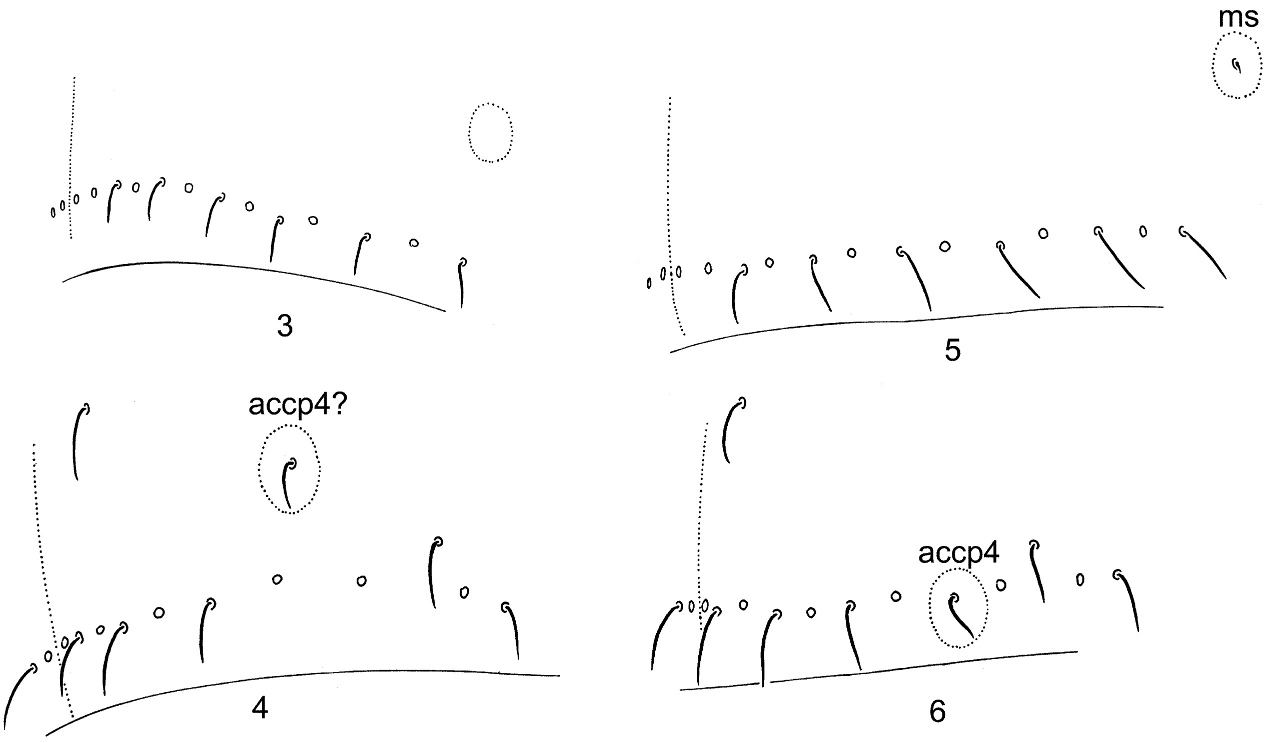
Material. Holotype female on slide and about 150 paratypes (10 on slide): South Africa: Western Cape: Cape Town: Table Mountain National Park, 10.iii.2009, native forest, in litter, sieving and extraction in Berlese funnel, near Wynberg cave (SAF-141, leg. Louis Deharveng & Anne Bedos); 4 paratypes on slide, ibid (RSA09-TBM001, leg. Charlene Janion); ibid, about 266 paratypes in alcohol, near Inchuk cave entrance (SAF-144, leg. Louis Deharveng & Anne Bedos).

Holotype and 140 paratypes in Iziko Museum (Cape Town, South Africa). 140 paratypes in MNHN (Paris, France); 140 paratypes in MSPU (Moscow, Russia).

Description. Body length from 0.6 to 1.0 mm. Pale with diffuse greyish pigment on body, eye spot black (Fig. 1). Ant.I with 4–5 sensilla ventro-laterally of which 2 long chaeta-like and 2–3 short, 3 basal microchaetae, 2 dorsal and 1 ventral (Figs 15, 17). Inner sensilla of AO III rather small. Ant.IV with 4 sensilla moderately thickened and several chaeta-like. Subapical microsensillum long curved at apex, subapical organite long, pin-like (Fig. 16).

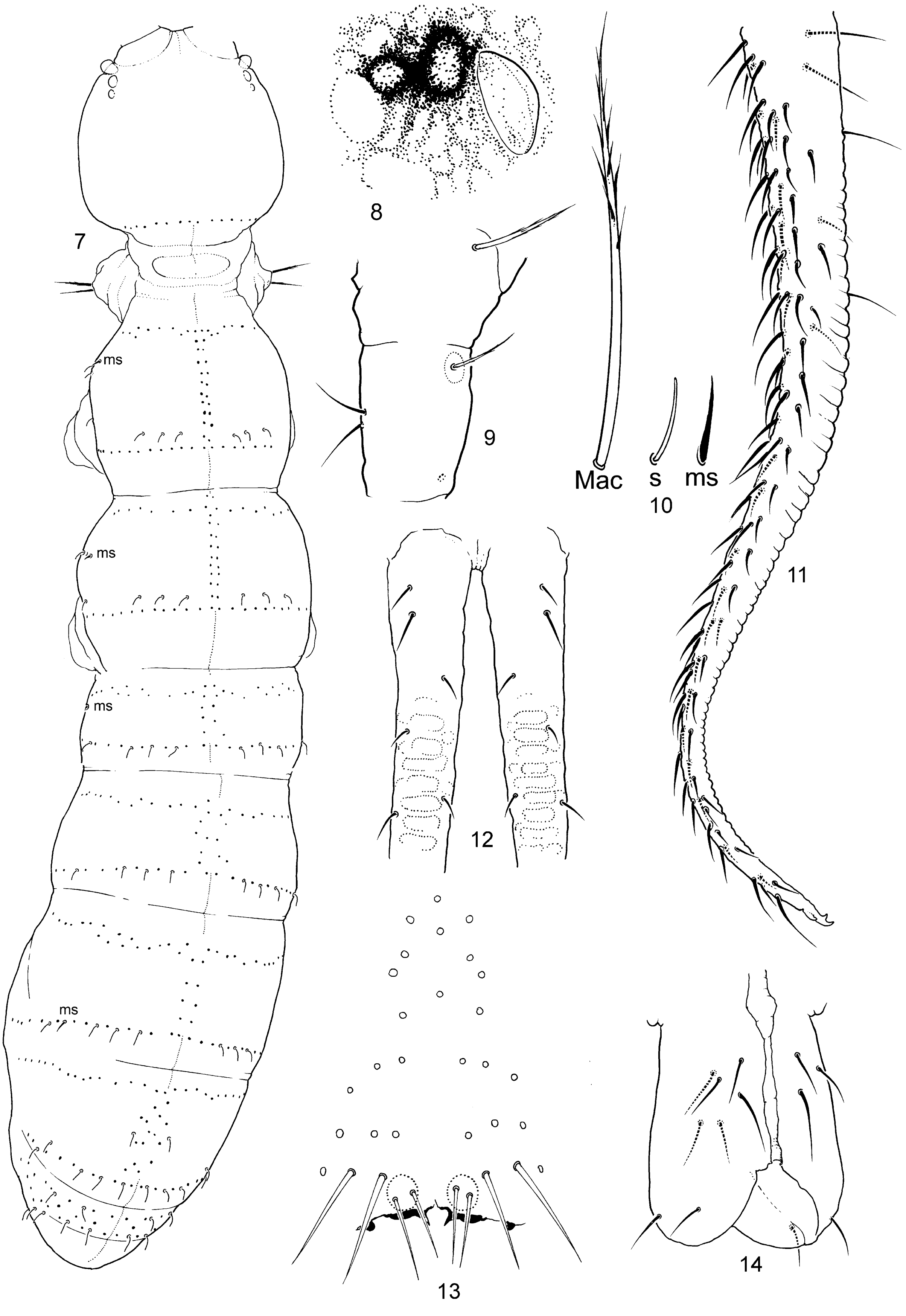


FIGURES 1–2. General habitus: 1, *P. sexsetosa* **sp. nov.**; 2, *P. obscurocellata* **sp. nov.**

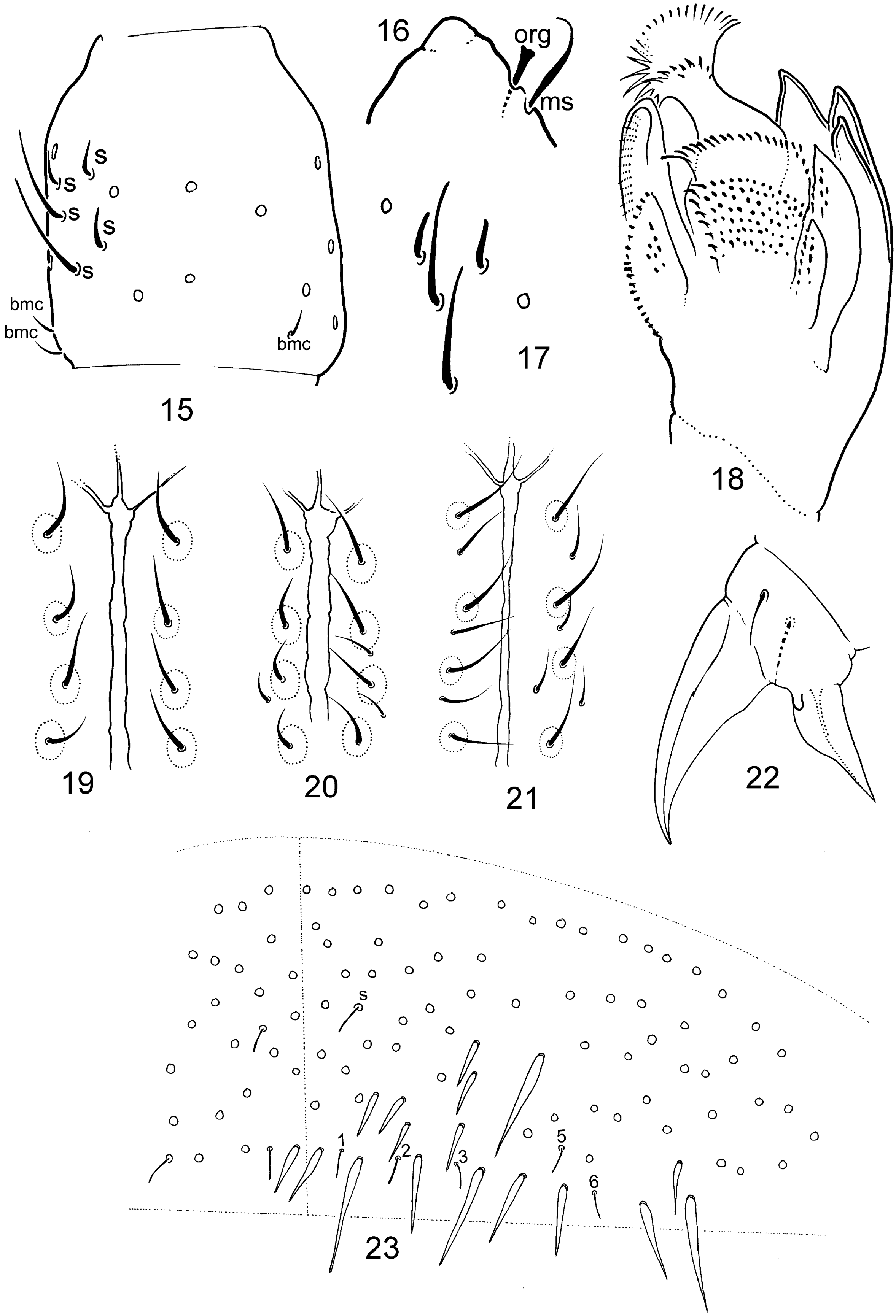


FIGURES 3–6. Basic sensorial pattern of South African (3–4, *P. obscurocellata* **sp. nov.**) and North Asiatic (5–6, *P. longa*) species; 3, 5, Abd.II; 4, 6, Abd.IV.

Two ocelli on each side of head, set together in a single eye spot, large anterior and smaller posterior (Fig. 8). Variation in this character was not found but eye pigmentation sometimes gives an impression of one large ocellus instead of two in dark coloured specimens. PAO wide, ca 1.4 as long as internal crest of Claw III. Labral formula 4/554, apical folds sharp, as in *P. notabilis*. Maxillary outer lobe with 4 sublobal hairs and trifurcate apical palp. Labial palp normal for family with 5 papillae (A–E) and full set of guards (16, including e7), lateral process as for



FIGURES 7–14. *P. sexsetosa* **sp. nov.**: 7, sensillar chaetotaxy of the body; 8, ocelli and PAO; 9, subcoxa of leg I; 10, elements of chaetom: macrochaeta (Mac), sensillum (s), microsensillum (ms); 11, dens, lateral view; 12, dens, posterior view; 13, manubrium, anterior view; 14, ventral tube.



FIGURES 15–23. *P. sexsetosa* **sp. nov.**: 15, Ant. I; 16, Ant.IV microsensillum and organite; 17, sensilla of first antennal segment; 18, maxillary head; 19–21, postlabial chaetae variations (different specimens); 22, claw and empodial appendage; 23, chaetotaxy of Abd.IV. 1–6: accp-sensilla.

family. Labium with 4 basomedian, 5 basolateral, and 4 proximal chaetae. Number of postlabial chaetae variable, from 4+4 to 8+8, including 4+4 large chaetae (always present) and usually several smaller ones between them. Asymmetrical variants 4+5, 4+6 or 5+6 common (Figs 19–21). Inner mouthparts as usual for the genus. Lamella 1 longer than capitulum with apex fan-shaped expanded, with marginal ciliation and one irregular row of long denticles on inner side. Lamella 6 with marginal ciliation and many irregular rows of denticles (Fig. 18).

Lower subcoxa of leg I with one outer chaeta (Fig. 9). Tibiotarsi of all legs with only 7 chaetae in apical whorl. Claw without clear internal teeth, with two minute lateral teeth (Fig. 22). Empodial appendage with broad lamella. Ventral tube with 2+2 lateral, 3–4+3–4 anterior, and 3–6 posterior chaetae (Fig. 14). Retinaculum with 4+4 teeth and 4(5) chaetae. Furcal subcoxa with 27–31 chaetae. Manubrial thickening simple. Anterior side of manubrium with numerous chaetae of which 2+2 shorter medial ones in its apical part (Fig. 13). Dens with numerous chaetae on anterior side and 6 chaetae on posterior side (2 basal, 2 median and 2 lateral) (Figs 11, 12). Mucro with 3 teeth.

Ordinary chaetae thickened (varies slightly between individuals), as usual for the genus (Fig. 10, 23). Axial chaetotaxy for Th.II, III normally with 12+12, 10+10 chaetae, respectively. Macrochaetae differentiated, ciliate, on last abdominal segments with more than 15 cilia, on Abd.V longer than length of tergite (as 1 : 1.1–1.3). Sensilla thin, well different from common chaetae, sensillary chaetotaxy on Th.II–Abd. V as: 2al+4accp, 1al+4accp / 4 accp, 4 accp, 4 accp, 1 am+5 accp, 2 am+5 accp. Comparing with full set of sensilla, 2 of them (accp4 and accp5) are missing on each side of segment from Th.II to Abd.III, and 1 sensillum (accp4) is missing on Abd.IV. Microsensilla (ms) 1,1/1,0,1 on Th.II–Abd.III. Microsensillum of Abd.III large, as long as sensillum (Fig. 10). Following the nomenclature of Potapov (1989) number of common chaetae in p-row between sensilla and microsensilla: 2s1s1s3s (Abd.I), 2–3s1s1s3–4s (Abd.II), 2–3s1s1s2–3ms1s (Abd.III), 1s1s1s2(s)1s (Abd.IV) (Figs 7, 23). Males present.

Distribution. Table Mountain National Park, Western Cape, South Africa.

Remarks. The species is well defined due to reduced sensillar chaetotaxy, six posterior chaetae on dens (shared with *P. obscurocellata* **sp. nov.**), 4–8 chaetae on each side in postlabial group on head, and enlarged microsensilla on Abd.III. As a rule, the species is well recognized superficially by two dark ocelli set together in a single eye spot of slightly variable size and shape.

Name derivation. Reflects the low number (6) of posterior chaetae on dens.

Parisotoma obscurocellata sp. nov.

Figs 2–4, 24–31.

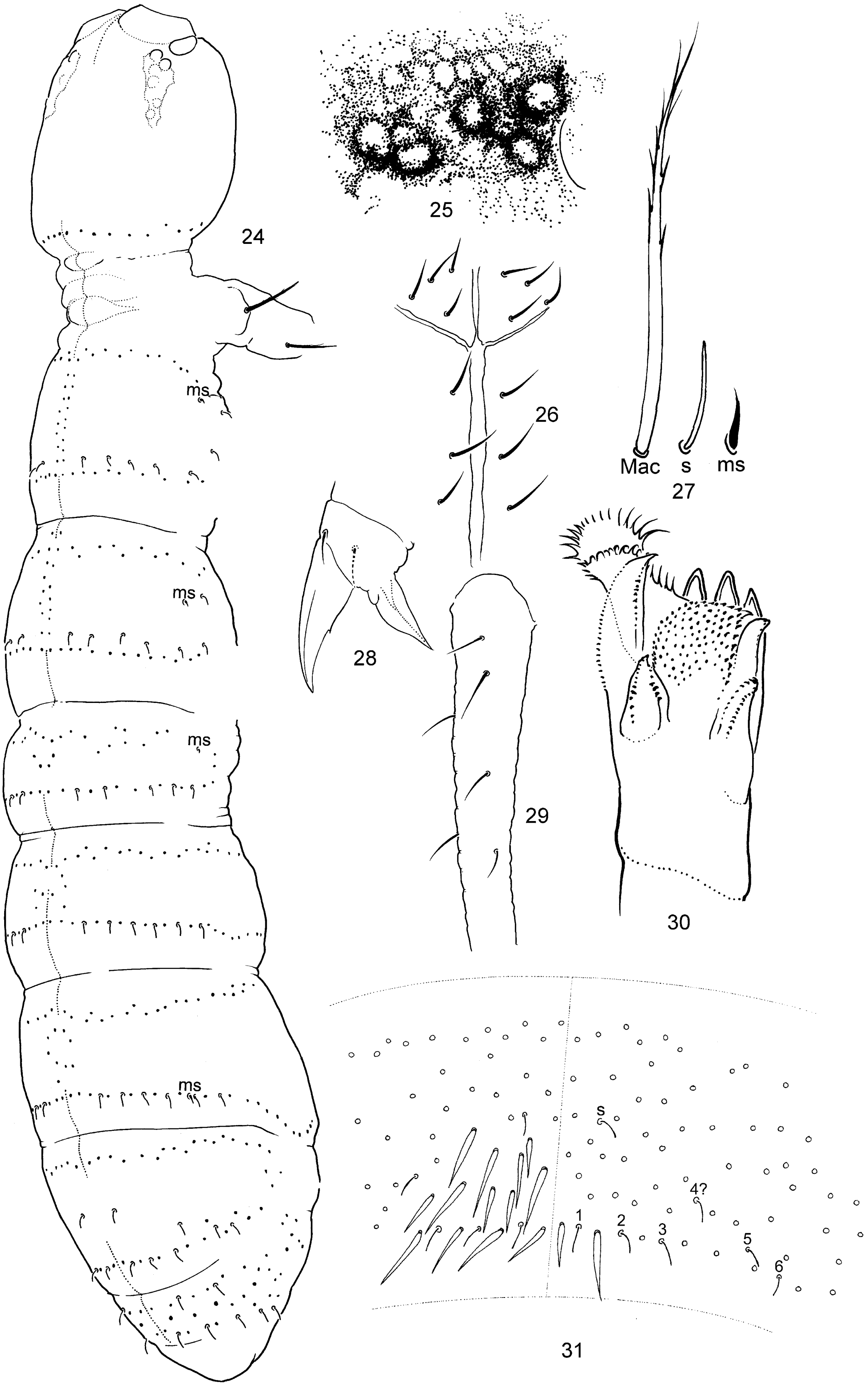
Type material. Holotype female on slide and about 60 paratypes (12 on slide, 48 in alcohol), South Africa, Western Cape, Kleinmond, Betty's Bay. 11.iii.2008, under creeping plants, extraction in Berlese funnels, legs. Louis Deharveng & Anne Bedos. (SAF-063).

Holotype and 20 paratypes kept in Iziko Museum (Cape Town, South Africa). 20 paratypes in MNHN (Paris, France); 20 paratypes in MSPU (Moscow, Russia).

Description. Body length about 0.8 mm. Pale with weak diffuse greyish pigment on corpus, eye spot black (Fig. 2). Ant.I usually with 4 sensilla ventro-laterally (2 long chaeta-like and 2 short), and 3 basal microchaetae (2 dorsal and 1 ventral). Inner sensilla of AO III of normal size. Ant.IV with 4 sensilla moderately thickened and several chaeta-like. Shape of subapical microsensillum long, slightly curved, and subapical organite not seen. At least 5 ocelli and less than 8 ocelli on each side of head, in divided eye spot, 3–4 in anterior larger group and 2–3 in smaller posterior (Fig. 25).

Exact number of ocelli difficult to see like in some other members of the genus, for example *P. notabilis*. PAO wide, 1.4 to 1.6 as long as internal crest of Claw III. Labral formula 4/554, apical folds as common for the genus. Maxillary outer lobe with 4 sublobal hairs and trifurcate apical palp (two specimens seen having bifurcate palp). Labial palp normal for family with 5 papillae (A–E) and 16 (15) guards (sometimes e7 lost on one side of the head). Labium with 4 basomedian, 5 basolateral, and 4 proximal chaetae. Invariably 3+3 postlabial chaetae (Fig. 26). Inner mouthparts as usual for the genus. Lamella 1 longer than capitulum with apex fan-shaped expanded, with marginal ciliation and one row of long denticles on inner side. Lamella 6 with many weak denticles in irregular rows (Fig. 30).

Lower subcoxa of leg I with one outer chaeta. Tibiotarsi of all legs with only 7 chaetae in apical whorl. Claw with clear internal tooth, lateral teeth uncertain (Fig. 28). Empodial appendage with broad lamella. Ventral tube with 2+2 lateral, 3+3 or 2+3 anterior, and 3 posterior chaetae. Retinaculum with 4+4 teeth and 2–3 chaetae. Furcal



FIGURES 24–31. *P. obscurocellata* **sp. nov.**: 24, sensillar chaetotaxy of the body; 25, ocelli; 26, postlabial and basomedian chaetae; 27, elements of chaetom: macrochaeta (Mac), sensillum (s), microsensillum (ms); 28, claw and empodial appendage; 29, dens, posterior; 30, maxillary head; 31, chaetotaxy of Abd. IV. 1–6: accp-sensilla.

subcoxa with 28–33 chaetae. Manubrial thickening simple. Anterior side of manubrium with numerous chaetae of which 2+2 shorter medial ones in its apical part. Dens with numerous chaetae on anterior side and 6 chaetae on posterior side (2 basal, 2 median and 2 lateral) (Fig. 29). Mucro with 3 teeth.

Ordinary chaetae thickened (Figs 27, 31). Axial chaetotaxy for Th.II, III 9–11+9–11. Macrochaetae differentiated, on Abd.V slightly longer than length of tergite (as 1 : 1.1), ciliate on last abdominal segment with up to 9 long cilia. Sensilla thin, well different from common chaetae, sensillar chaetotaxy on Th.II–Abd. V as: 2al+6accp, 1al+6accp / 6 accp, 6 accp, 6 accp, 1 am+6 accp, 2 am + 5 accp. Rarely one of accp-sensilla lost on half of tergite (specimens with 5 accp-sensilla on either Th.II, Abd.I, Abd.II, and Abd.IV seen). Microsensilla (ms) 1,1/1,0,1 on Th.II–Abd.III. Microsensilla of Abd.III normal, about half as long as sensilla (Fig. 27). Following the nomenclature of Potapov (1989), number of common chaetae in p-row between sensilla and microsensilla: 2–3s1s1s1s1s (Abd.I), 3s1s1s1s1s (Abd.II), 3s1s1s1ms0s1s (Abd.III), 1s1s1s1(s)1(s)1s (Abd.IV) (Fig. 24, 31). Males not seen.

Distribution. Betty's Bay area, Western Cape, South Africa.

Remarks. The species is readily identified by six posterior chaetae on dens and many ocelli arranged in two eye spots. The former character was seen only in two other undescribed species from South Africa and never seen in Northern Asiatic forms. The latter character makes the identification of *P. obscurocellata* easy even under low magnification. *P. greensladeae* (1+1 ocelli, Australia) is possibly related with the new species sharing presence of inner tooth on claw, same chaetotaxy of ventral tube and full sensillar set on Abd.IV. The new species differs from *P. sexsetosa* **sp. nov.** by full sensillar set (87/66677 vs. 65/44467), fewer postlabial chaetae (3+3 vs. 4+4 or more), number of ocelli (5+5 or more vs. 2+2) and inner tooth on claw (present vs. absent). The very briefly described *Isotoma mossopi* Womersley, 1934 from South Africa (Namibia) belongs to *Parisotoma*, too. It has also a large ocular spot but with only four ocelli according to the original figure. Moreover, the empodial appendage is thinner than in *P. obscurocellata*.

Generic assignment of the new species is not fully understood. Elongated eye spot with many ocelli (but fewer than 8) places it formally closer to genus *Desoria* Nicolet. All other characters, especially seven chaetae in apical whorl on tibiotarsi, few chaetae on appendages, sensillar set, maxillary shape indicate genus *Parisotoma*. The taxonomical value of number of ocelli, a character of adaptive nature, calls for reconsidering the diagnosis of the genus *Parisotoma*.

Name derivation. The species is named after the number of eyes which are difficult to observe.

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References

Bagnall, R.S. (1940) Notes on British Collembola. *The Entomologist's Monthly Magazine*, 76, 163–174.

Barra, J.-A. (1995) Nouveaux Collemboles Poduromorphes des sables littoraux (partie terrestre) de la Province du Natal (Rép. Sud Africaine) (Insecta: Collembola). *Journal of African Zoology*, 109, 125–139.

Barra, J.-A. (1997) Nouveaux Collemboles Entomobryomorphes des sables littoraux (partie terrestre) de la Province du Natal (Rép. Sud Africaine) (Insecta: Collembola). *Journal of African Zoology*, 111, 465–480.

Barra, J.-A. (2001) *Proisotoma davidi* sp. n. from Cape Province (South Africa) (Collembola). *Deutsche Entomologische Zeitschrift*, 48, 23–26.

Deharveng, L. (1981) Collemboles des Iles subantarctiques de l'Océan Indien. Mission J. Travé 1972–1973. *Biologie des Sols, CNFRA*, 48, 33–108.

Paclt, J. (1959) Collembola. South African Animal Life. *Results of the Lund University Expedition in 1950–1951*, VI, 24–78.

Paclt, J. (1967) On South and Central African Collembola. *Journal of the Entomological Society of Southern Africa*, 29, 135–47.

Potapov, M. (1989) The use of sensorial chaetotaxy in taxonomy of some Isotomidae (Collembola). *In*: Dallai, R. (Ed.), *Proceedings of the Third International Seminar on Apterygota, Siena*, University of Siena, Italy, pp. 35–42.

Potapov, M. (1991) Species of the genus *Isotoma* subgenus *Parisotoma* Bagnall, 1940 and *Sericeotoma* subgen. nov. (Collembola, Isotomidae) of USSR fauna. *Acta zoologica cracoviensia*, 34, 267–301.

Rusek, J. (1984) New species and review of the *Isotoma notabilis* species-group (Collembola, Isotomidae). *Acta Entomologica Bohemoslovaca*, 81, 343–369.

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ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Variation in decomposition rates in the fynbos biome, South Africa: the role of plant species and plant stoichiometry

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Abstract Previous studies in the fynbos biome of the Western Cape, South Africa, have suggested that biological decomposition rates in the fynbos vegetation type, on poor soils, may be so low that fire is the main factor contributing to litter breakdown and nutrient release. However, the fynbos biome also comprises vegetation types on more fertile soils, such as the renosterveld. The latter is defined by the shrub *Elytropappus rhinocerotis*, while the shrub *Galenia africana* may become dominant in overgrazed areas. We examined decomposition of litter of these two species and the geophyte *Watsonia borbonica* in patches of renosterveld in an agricultural landscape. In particular, we sought to understand how plant species identity affects litter decomposition rates, especially through variation in litter stoichiometry. Decomposition (organic matter mass loss) varied greatly among the species, and was related to litter N and P content. *G. africana*, with highest nutrient content, lost 65% of its original mass after 180 days, while *E. rhinocerotis* had lost ca. 30%, and the very nutrient poor *W. borbonica* <10%. Litter placed under *G. africana* decomposed slightly faster than when placed under *E. rhinocerotis*. Over the course of the experiment, *G. africana* and *E. rhinocerotis* lost N and P, while *W. borbonica* showed strong accumulation of these elements. Decomposition rates of *G. africana* and *E. rhinocerotis* were substantially higher than those previously reported from fynbos vegetation, and variation among the species investigated was considerable. Our results suggest that fire may not always be the main factor contributing to litter breakdown and nutrient release in the fynbos biome. Thus, biological decomposition has likely been underestimated and, along with small-scale variation in ecosystem processes, would repay further study.

Keywords Ecosystem functioning · Fynbos · Nutrient release · Renosterveld · Soil ecology

Introduction

In terrestrial systems, plant species composition affects herbivores and decomposers and the processes for which they are responsible. This is mediated at least partly by variation and complexity in plant chemistry due to secondary plant metabolites and plant stoichiometry (Enríquéz et al. 1993; Wardle 2002; Sudderth et al. 2005; Osler and Sommerkorn 2007). Traditionally, nitrogen (N) has been regarded to be the key limiting element in terrestrial systems (Vitousek and Howarth 1991; Ågren and Bosatta 1996), while phosphorus (P) plays a much more important role in limnetic systems (e.g. Schindler 1977). However, production in many terrestrial systems can also be influenced by P-limitation (Elser et al. 2007), especially in

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geologically older areas which never have been subjected to glaciation or aeolian deposits, such as Hawaii (Vitousek 2004) and South Africa (Richards et al. 1997, but see also Witkowski 1989). In addition, even if N is a limiting factor for primary production in a system, herbivory and litter decomposition processes may still be influenced significantly by other aspects of plant stoichiometry, such as P content (Hobbie and Vitousek 2000).

Differential effects of species at the scale of individual plants may be important for spatial variation and heterogeneity in ecosystems. It may create a mosaic structure of ecosystem processes even within vegetation types (Usher et al. 1982; Saetre and Bååth 2000; Ettema and Wardle 2002; Whitham et al. 2003). Below-ground variation in the quality and quantity of litter originating from different plant species may contribute to spatial variation in decomposition and nutrient cycling as well as to soil community structure (De Deyn et al. 2004; Wardle 2005; Viketoft et al. 2009). Individual plant species within a vegetation type can in different ways affect microbial communities and thereby decomposition rates on a small scale (Loreau 1998; Ehrenfeld et al. 2005). Decomposer communities may be adapted to litter fall on the spatial scale of individual plants, resulting in higher decomposition rates of a specific litter type under the plant species from which it originates (Ayres et al. 2009). Alternatively, plant species produce litter of different stoichiometry, which in itself may affect decomposition rates substantially (Enríquéz et al. 1993; Sterner and Elser 2002).

The Western Cape of South Africa is characterized by the hyperdiverse vegetation of the fynbos biome (Cowling and Lombard 2002; Linder 2003; Mucina and Rutherford 2006; Thuiller et al. 2006). Typical fynbos vegetation occurs on poor, sandy or stony soils (Mucina and Rutherford 2006). It is characterized by Proteaceae, ericoid shrubs, and the reed-like Restionaceae, which have low nutrient content and produce slowly decomposing litter (Mitchell et al. 1986; Witkowski 1991). Previous studies have suggested that biological decomposition is so low that litter accumulates on the ground for years, until it is consumed by the periodic fires typical of this vegetation type. Consequently, it has been argued that fire is a major factor for litter decomposition and nutrient cycling in fynbos vegetation (Mitchell 1983; Mitchell et al. 1986; Stock and Lewis 1986; Stock and Allsopp 1992).

The fynbos biome, however, also includes other vegetation types, one of the most significant being the renosterveld, which is also fire-prone. It occurs on richer, more developed and clay-rich soils, e.g. in valleys and on river plains, and, in contrast to the typical fynbos vegetation, includes few proteoids, ericoids and restioids (see Mucina and Rutherford 2006). Renosterveld used to constitute about 30% of the fynbos biome (Mucina and Rutherford 2006), but as it occupied the most fertile soils of Western Cape, it has long been under pressure from agriculture and urban development (Kemper et al. 1999; Rouget et al. 2003). The restricted remains of this formerly extensive vegetation type are highly fragmented and often strongly influenced by grazing from cattle and sheep. The defining plant species of this vegetation type is the renosterbos *Elytropappus rhinocerotis* (Asteraceae), which is an abundant and conspicuous shrub. Other important elements in this vegetation type are asteraceous shrubs, and a rich geophyte flora (Mucina and Rutherford 2006). *Elytropappus rhinocerotis* is unpalatable to livestock (Proksch et al. 1982), and thus it may be favoured by grazing, as is certainly true of the yellowbush (*Galenia africana*), which has become a dominant species in many disturbed and overgrazed areas (van der Lugt et al. 1992; Allsopp 1999).

Generalisations about ecological processes in the fynbos biome, such as the role of fire in litter decomposition (Mitchell et al. 1986; Mitchell and Coley 1987), have largely been based on studies of the typically nutrient-poor fynbos. Much less ecological work has been done in renosterveld (but see, e.g., Donaldson et al. 2002), and very little is known about the belowground processes in this vegetation type (Stock and Allsopp 1992). The differences in plant productivity and soil properties between the typical fynbos and the renosterveld may affect plant stoichiometry and thereby have consequences for decomposition and nutrient dynamics.

In this study, we compare decomposition of litter, measured as mass loss from litter bags, from selected plant species in renosterveld. In particular, we examine to what extent decomposition dynamics of litter from different species can be predicted from their stoichiometry, and the shrub species under which they are placed. We chose to focus on two herbaceous shrubs common to the renosterveld, *E. rhinocerotis* and *G. africana*, which both have considerably higher N and P content (personal observations) than typical fynbos plants (Mitchell et al. 1986), and also differ between each other in stoichiometry (see below). In addition, we included a geophyte, *Watsonia borbonica* (Iridaceae), as a representative of the rich geophyte flora typical of renosterveld (Mucina and Rutherford 2006). The results are compared with previous studies of decomposition in fynbos. The study is part of a larger project examining soil animal diversity and ecosystem processes in the fynbos biome.

Materials and methods

We recorded mass loss of litter placed in the field in small containers (plastic litter bags), designed to examine both soil animals and decomposition, for 6 months during the South African winter in 2007 (March–September).

Study sites

Two study sites with remnant patches of renosterveld vegetation were chosen in an agricultural landscape north of Piketberg, approximately 200 km N of Cape Town, South Africa. The area has typical Mediterranean climate with cool, moist winters and hot, dry summers (Online Resource, Appendix 1). The two farms, Meerlandsvlei and Renosterhoek, grow mainly wheat and canola. Both also have livestock, grazing being most intense at Renosterhoek. Parts of the farms contain areas with semi-natural vegetation, mainly renosterveld. Although most grazing occurs on the farmed fields, the renosterveld patches were also somewhat affected. Two such patches with both *G. africana* and *E. rhinocerotis* bushes were selected. Both study sites were within 50 m of farmed fields, as most of the patches with natural vegetation in this area are small (from 10 to 200 m in diameter; mean area approx. 10 ha).

The site at Renosterhoek (32°32.146′S, 18°49.393′E) was an approximately 1-ha area that was moderately grazed when the study commenced. The shrub layer was dominated by *E. rhinocerotis*, interspersed with a large number of *G. africana* bushes. The ground layer had both grasses and forbs. The Meerlandsvlei site (32°34.189′S, 18°53.009′E) was a smaller patch, <0.5 ha, and had a more species-rich shrub layer, but with both *G. africana* and *E. rhinocerotis* occurring commonly. Bare ground was common at both sites during the dry season, but by the end of the study period in August–September, it was largely covered by annual plants, mainly forbs. The size and vegetation of the two selected patches can be considered representative of the large number of small patches with semi-natural vegetation in the renosterveld of the Swartland area north of Cape Town and elsewhere (see Donaldson et al. 2002). None of the sites had burned during the years preceding the study, but on Meerlandsvlei some parts of the patch bordering the wheat fields were accidentally burned in early May, resulting in a loss of traps from two pairs of bushes (see below).

Plant species, litter collection and treatment

Three plant species were chosen for study. Renosterbos, *Elytropappus rhinocerotis* (Asteraceae), is the defining plant species for the renosterveld vegetation type (Mucina and Rutherford 2006). It is a common, evergreen, resinous shrub, up to 2 m tall and with scale-like dark green leaves. It occurs on more fertile clay, shale and sandstone soils over much of the Western Cape (Manning 2007). It is rich in phenolics (Proksch et al. 1982), and has been used for infusions in traditional medicine (van Wyk et al. 2000). Its resin exhibits anti-herbivore properties by acting as a tannin-like compound (Proksch et al. 1982). The plant material used in this study was obtained from a stand close to Stellenbosch, and had C:N = 52.4, and C:P = 810.

Galenia africana (Aizoaceae) is also a common shrub in the Western Cape, up to 1.5 m tall. It is an indicator of disturbance such as overgrazing (Allsopp 1999; Todd and Hoffmann 1999), has a complex set of secondary compounds and is toxic to sheep and goats (Van der Lugt et al. 1992; Vries et al. 2005). It has been argued to enrich and stabilize soils under its canopy, producing fertile islands with higher levels of nitrogen and available phosphorus (Allsopp 1999; Simons and Allsopp 2007). This species was collected from an overgrazed rangeland west of the Paarl mountain, where it was the dominant shrub in the vegetation. It had a higher nutrient content than *E. rhinocerotis* (C:N = 23.0, and C:P = 367).

The geophyte *Watsonia borbonica* (Iridaceae) is a robust, branched, 50- to 200-cm-tall perennial with firm leaves which turn brown by the end of summer. It occurs on sandstone, granite and clay in the southwestern Cape (Manning 2007). The species represents the sturdier elements of the rich geophyte flora in the Western Cape, and may be quite numerous in renosterveld patches (personal observation). Although it is not listed by Mucina and Rutherford (2006) as a species typical of renosterveld in the Piketberg area, the similar, congeneric geophyte, *Watsonia marginata*, is an important element in this area. However, for conservation reasons, we did not include material of this species, nor of representatives of the short-lived seasonal or annual geophytes, most of which flower in spring and disappear shortly afterwards. *Watsonia borbonica* litter was collected in an area dominated by this species in the Jonkershoek Nature Reserve, 10 km SE of Stellenbosch. It had the lowest nutrient content of the three studied species (C:N = 133, and C:P = 8,277). The chemical composition of all plant materials used is given in Online Resource, Appendix 2.

Plant material of *E. rhinocerotis* and *G. africana* was collected on 6–7 March 2007, at the end of the dry season, by cutting the outer 10–20 cm of branches of healthy shrubs. The material was taken to the laboratory, dried at 40°C for at least 24 h, and then stored in open containers at room temperature. We separated the leaves and outermost (1–2 cm) thin branches from the coarser material, and cut this into approximately 1-cm-long pieces. *Watsonia borbonica* was collected on 7 March by taking whole leaves from the plants. The leaves were cut into approx. 1 × 1 cm pieces and dried at room temperature for 5 days. For each species, the air-dried litter was mixed thoroughly and then stored dry at room temperature until placed in the litter bags. To estimate initial nutrient content, dry mass and ash-free dry mass, six randomly selected samples of each species were taken when the litter bag traps were being filled.

The litterbags constituted individually numbered cylindrical plastic containers with a height of 4 cm and a diameter of 7.5 cm. The bottom consisted of a steel net with mesh size 0.5 mm. The traps had a removable lid with 1.6-mm mesh size to allow animals to enter the trap. In the laboratory, the traps were filled with air-dried litter up to approx. 3.5 cm, which had been weighed to nearest 0.1 mg on an electronic balance (FA304T; Avery Berkel, Fairmont, USA). The litter was not compressed and was allowed to maintain its normal volume and density. Average litter dry mass per trap was: *G. africana* 16.33 g (range 15.38–17.34), *E. rhinocerotis* 9.91 g (range 9.42–10.51) and *W. borbonica* 8.76 g (range 8.09–9.57), corresponding to on average 13.81, 9.51 and 8.54 g of organic matter, respectively. The filled traps were stored dry at room temperature before being deployed in the field on 14 March 2007.

Experimental design

To examine the differences in decomposition rate and nutrient dynamics among the three litter types, and to test if there was effect of the bush species under which litter was placed on decomposition rate, we placed three sets of three litterbag traps under five bushes of *G. africana* and five bushes of *E. rhinocerotis* at each of the two sites. Each set contained one trap of each litter type. The bushes were chosen to ensure that both bush species were interspersed over the whole study site, to avoid confounding the bush effect with unmeasured environmental gradients. Coordinates for each bush was obtained by GPS.

The traps were placed under the bushes, less than 40 cm from the bush base, on the southwest to southeast side to minimise sun exposure. They were placed in the soil with the top of the trap at ground level. The traps in each set were placed within 3–4 cm from each other, while the distance between sets under a bush was at least 10 cm.

An accidental burning destroyed 24 of the traps at Meerlandsvlei. In addition, 4 traps at Renosterhoek were dug up by animals, 4 traps were flooded at Meerlandsvlei, and 4 traps were lost for unknown reasons. The data set thus comprises 146 of the original 180 traps, but the losses were not much more common for one litter type or bush species (Table 1).

Collection of traps and laboratory treatment

To examine mass loss variation over the season, the litterbags were sampled at three times: 18 May, 27 July and 12 September 2007, i.e. after 65, 131 and 182 days in the field. At each sampling period, one randomly selected set of traps was collected from each bush, while the remainder were left for later collection. When traps were collected, they were taken out of the soil, wrapped in aluminium foil and immediately placed individually in plastic bags and stored cool, in an upright position in thermally insulated containers, until they were returned to the laboratory on the same evening. They were then stored at 8–10°C for 1–7 days.

Table 1 Decomposition rate (*k* values) of litter of the three renosterveld plant species, *Galenia africana* (G), renosterbos *Elytropappus rhinocerotis* (R) and *Watsonia borbonica* (W)

Litter type	*k* value (day^{-1})	SE	*n*	Half-life (days)	SE	*n*
G	0.00674	0.00012	50	101.2	151.5	36
R	0.00222	0.00012	47	308.4	151.5	34
W	0.00029	0.00012	49	2,032	151.5	35

Values are mean *k* values (decomposition constant in the exponential decay model; unit g g^{-1} organic matter day^{-1}) and mean mass half-life (in days) for the three litter types across the three sampling days. Only the effect of litter type is shown because variation due to this factor was far greater than for all other factors (as shown in Table 2). Half-life values do not include data from sampling day 65 because of a number of negative mass loss values for *W. borbonica* (indicating increased mass; see text)

Before chemical analysis, soil animals were extracted from the samples (results not presented here). The dry litter samples in each trap were then gently transferred to aluminium foil and dried at 50° for at least 24 h to ensure that the samples were dry before storage. Little organic material was lost during the extraction process. The dried samples were individually packed in aluminum foil and plastic bags, and sent to Sweden for determination of mass loss and chemical composition.

Mass loss was determined as loss of organic matter from the traps. Dry weight was determined by weighing samples before and after heating at 105°C for 24 h. Ash-free dry weight was determined after heating at 550°C. The difference between ash-free dry weight and dry weight was used as the measure of organic matter in the material. Many traps had accumulated mineral soil particles during the study period, which was accounted for by this procedure.

Total C and N concentrations in the dried material were determined using a Carlo-Erba NA 1500 Elemental Analyzer (Strumentazione, Milan, Italy). Phosphorus (P) and K, Na, Mg and Ca were measured by Inductively Coupled Plasma Atomic Spectroscopy (Optima 3000; PerkinElmer, Waltham, MA, USA) after wet combustion of 400 mg ground material in nitric and percloric acid.

Statistics

Mass loss of organic matter was measured by the decomposition constant *k* calculated assuming the exponential decomposition model (Olson 1963), i.e.

$$W_t = W_0 e^{-kt} \tag{1}$$

where W_0 is the mass of organic matter at the start of the experiment and W_t is the mass of organic matter at time t. The constant k has the unit day^{-1} and was calculated for each litter bag for each sampling day, which was the variable used in the statistical analysis. We also calculated half-life of litter 0.693 k^{-1}, turnover time of litter k^{-1}, and the proportion of organic matter lost at each sampling day (Olson 1963). Carbon to nutrient ratios were calculated on a weight basis using the data from the chemical analyses. All ratios were square-root-transformed before statistical analysis, while k values were untransformed.

We analysed the data with a General Linear Mixed Model (GLMM) using SAS procedure Mixed. The fixed factors in the model were at level 1 Farm, Bush species and their interaction Farm × Bush species, at level 2 Litter type and its interactions with the above factors, and at level 3 Sampling day and its interactions with all the factors above. The error term when testing effects of factors at level 1 was Farm × Bush species × Bush number, at level 2 the error term was Litter × Farm × Bush species × Bush number, and at level 3 the residual error. The full model is given in Table 2, and was used for all dependent variables. Degrees of freedom were estimated with the Satterthwaite method.

Results

Decomposition

Litter type was by far the most important factor explaining variation in decomposition rate, measured as loss of organic matter from the litterbags (Tables 1, 2). *Galenia africana* litter decomposed most rapidly, with less than 40% of the original organic matter mass remaining after 131 days, but with little further decomposition in the following months (Fig. 1). By contrast, *E. rhinocerotis* had lost ca. 30% of the original mass after 182 days, while the *W. borbonica* litter had decomposed very slowly with less than 10% of the original mass lost at the end of the study. In fact, the amount of organic material in *W. borbonica* litterbags increased slightly during the first time period (from March to May, Fig. 1; one-sample t test if mass loss is negative and differs from 0, $p = 0.0085$, $n = 14$) and decreased only from May onwards.

Half-life of litter ranged from 100 days for *G. africana* to more than 5 years for *W. borbonica* litter (Table 1). Turnover of litter was 0.4 years for *G. africana*, 1.2 years for *E. rhinocerotis* and 8.6 years for *W. borbonica*. However, because these values were calculated for the first 182 days of decomposition only, the degree of uncertainty in the estimates is fairly high, with the exception of the fast decomposing *G. africana*.

The temporal pattern in decomposition rates (k values) during the experiment differed between species, as indicated by the significant Litter type × Sampling day interaction (Table 2). All litter types showed an increase in decomposition rate from May to July (Days 65–131; data not shown). However, *G. africana* then showed a subsequent strong decrease in decomposition rate from July to September (Days 131–182; Fig 1). Evidently, most of the

Table 2 Statistical (GLMM) analysis of decomposition rate in relation to the fixed factors farm, bush species, litter type and sampling day

Factor	*df*	*F*	*P*
Farm	14.6	2.75	0.1183
Bush species	14.6	2.38	0.1440
Bush species × Farm	14.6	4.18	0.0593
Litter type	29.5	1,108.4	<0.0001
Litter type × Bush species	29.5	0.06	0.9411
Litter type × Farm	29.5	2.82	0.0756
Litter type × Bush species × Farm	29.5	2.71	0.0833
Sampling day	77.1	30.84	<0.0001
Sampling day × Bush species	77.1	0.87	0.4212
Sampling day × Farm	77.1	0.88	0.4178
Sampling day × Bush species × Farm	77.1	1.27	0.2873
Litter type × Sampling day	79.2	13.69	<0.0001
Litter type × Bush species × Sampling day	79.2	0.39	0.8169
Litter type × Farm × Sampling day	79.2	0.53	0.7170
Litter type × Bush species × Farm × Sampling day	79.2	1.25	0.2971

The table shows the results from a General Linear Mixed Model analysis of the decomposition constant (k values in Table 1) in relation to the fixed factors Farm, Bush species (i.e. the bush species under which litters were placed; *G. africana* or *E. rhinocerotis*), Litter type (i.e. the litter collected from the three species *G. africana*, *E. rhinocerotis* or *W. borbonica*) and Sampling day (65, 131 or 182 days from the start of the experiment)

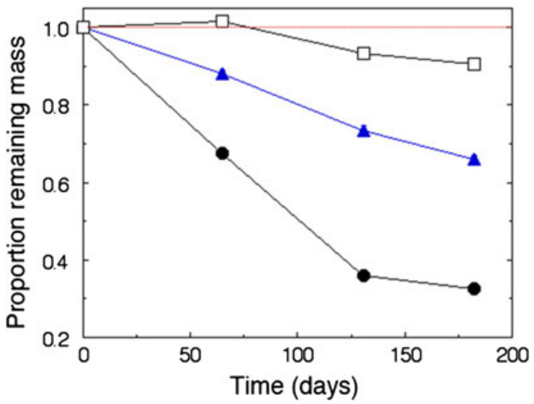


Fig. 1 Mass loss in three litter types in relation to time during the South African winter 2007. *Galenia africana* (*filled dots*), renosterbos *Elythropappus rhinocerotis* (*filled triangles*) and *Watsonia borbonica* (*open squares*). Mass loss differed significantly between the litter types (Tables 1 and 2). Day 0 = 14 March 2007. Standard *error bars* are smaller than the *dots*

most readily decomposed parts of this litter had disappeared well before the last sampling day.

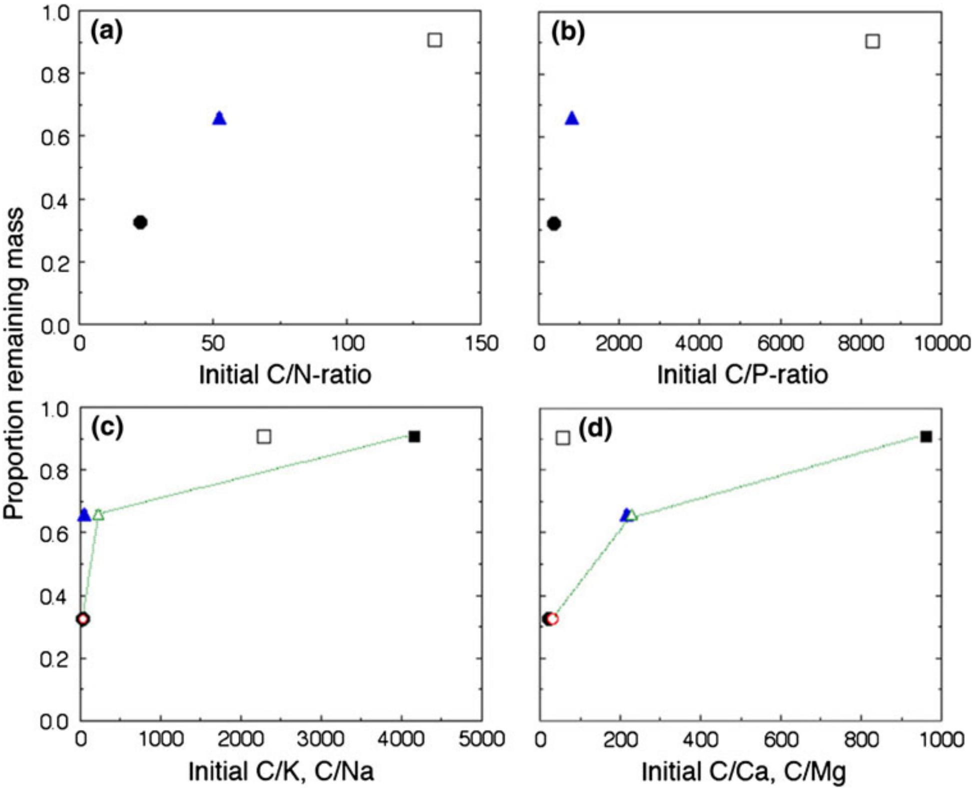
There was no indication that decomposition was slower when litter of one species was placed under plants of another species. The Bush species × Litter type interaction was far from significant in the analyses of decomposition rate (e.g. Table 2). On the contrary, decomposition of all litters appeared to be somewhat faster (on average 8%) when placed under *G. africana* than under *E. rhinocerotis*, but the effect varied between the two farms as reflected in the Bush species × Farm interaction term (Table 2).

Figure 2 shows the relations between initial plant material chemical composition and mass loss. *Galenia africana*, which decomposed fastest, had the highest initial concentrations of N, P, Na and Mg while the very slowly decomposing brown *W. borbonica* had by far the lowest concentration of the same nutrient elements. Furthermore, the intermediate litter type, *E. rhinocerotis,* followed similar relationships between the concentrations of these elements and their decomposition rates. To summarise, we found lower mass loss with increasing C/N and C/P ratios, as well as for C/Na and C/Mg ratios, while initial C/K and C/Ca ratios showed no clear relation to mass loss.

Stoichiometry during decomposition

Plant litter stoichiometry showed significant temporal changes in all litter types. It also differed substantially between litter types (Fig. 3; Online Resource, Appendices 2–3). In all litter types, N and P concentrations increased over time, as shown by the decreasing C/N and C/P ratios (Fig. 3a, b). This was most evident in *W. borbonica* litter, and in particular for the C/P ratio (Fig. 3b). The patterns of

Fig. 2 Remaining mass at the end of the study period (day 182) in relation to carbon to nutrient ratios of the original material. **a** C/N, **b** C/P, **c** C/K and C/Na, and **d** C/Ca and C/Mg. Notation: **a** and **b** *Galenia africana* (*filled dots*), renosterbos *Elythropappus rhinocerotis* (*filled triangles*) and *Watsonia borbonica* (*open squares*); **c** and **d** as above for K and Ca, while for Na and Mg the *dots* are connected by *lines*, and *G. africana* (*open dot*), *E. rhinocerotis* (*open triangle*) and *W. borbonica* (*filled square*), Standard *error bars* are smaller than the *dots*



change in K, Na, Mg and Ca varied between the four elements and four litter types. C/K and C/Na ratios increased with time in *G. africana* and *E. rhinocerotis*, indicating higher losses of these elements than expected from mass loss. By contrast, *W. borbonica* litter showed decreasing C/K and C/Na ratios over time (Fig. 3c, f). Decreased C/Mg ratios over time were found for all litter types except *G. africana* (Fig. 3e). Levels of and changes in C/Ca appeared to be unrelated to the other elements. *G. africana* litter showed the lowest C/Ca ratios, as expected, but *W. borbonica* litter had lower C/Ca ratios than *E. rhinocerotis*, which was the most Ca poor litter during the whole study period (Fig. 3f).

The plant litter types varied in the dynamics of N and P (Fig. 4). In *G. africana* litter, despite a decrease in C/N ratio, more than half of the original nitrogen (57%) had been mineralised and lost from the litterbags during the study period. Much less nitrogen had been mineralised from *E. rhinocerotis* litter (15%) while in the *W. borbonica* litter, N had accumulated during the same period (Fig. 4a). Similarly, there had been a marked loss of P from *G. africana* and *E. rhinocerotis* litter. The brown *W. borbonica* litter differed fundamentally from the other litter types by a strong accumulation of P, that must have been obtained from the surroundings (Fig. 4b). Nutrient concentrations were higher in litter placed under *G. africana* bushes than in litter placed under *E. rhinocerotis* (Online Resource, Appendix 3).

Discussion

Earlier studies have suggested that decomposition of typical fynbos plants is very slow (Mitchell et al. 1986; Mitchell and Coley 1987; Witkowski 1991; Stock and Allsopp 1992). Our study showed considerably higher decomposition rates than found in these previous studies (Table 3). One possible explanation for these contrasting results is that decomposition is generally faster in the more nutrient-rich renosterveld than in typical fynbos vegetation, which grows on nutrient-poor soils (e.g. Witkowski 1991; Mucina and Rutherford 2006; Manning 2007). However,

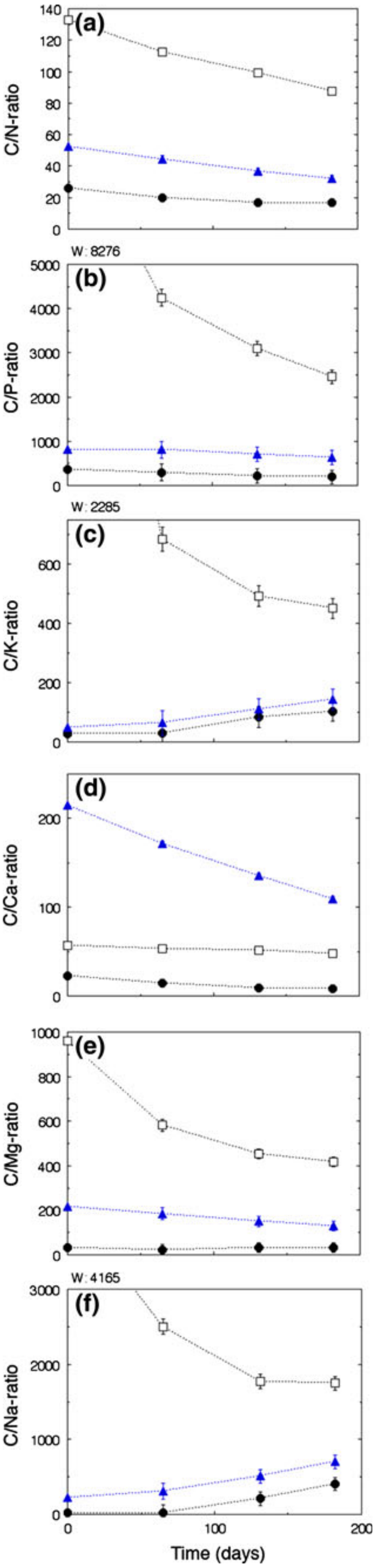


Fig. 3 Temporal changes in carbon to nutrient ratios in three litter ▶ types: *Galenia africana* (G, *filled dots*), renosterbos *Elythropappus rhinocerotis* (R, *filled triangles*) and *Watsonia borbonica* (W, *open squares*). See Online Resource, Appendix 3 for results from statistical analyes. Standard *error bars* when not visible are smaller than the *dots*. **a** C/N-ratio in litter types G, R and W decreased with time. **b** C/P-ratio in litter types G, R and W decreased with time. **c** C/K-ratio in G and R increased with time, while it decreased in W. **d** C/Ca-ratio in all litter types decreased with time. **e** C/Mg-ratio in R and W decreased with time, but did not change in G. **f** C/Na-ratio in G and R increased with time while W decreased

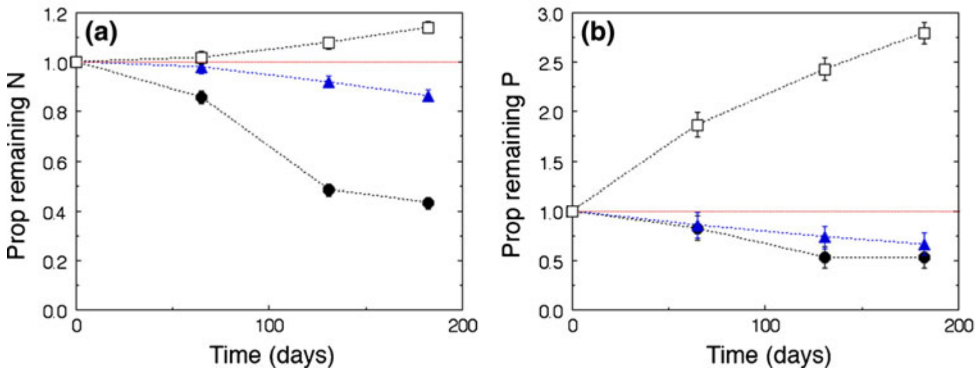


Fig. 4 Changes in proportion of original amounts of **a** N and **b** P in litterbags over time. *Galenia africana* (*filled dots*), renosterbos *Elythropappus rhinocerotis* (*filled triangles*) and *Watsonia borbonica* (*open squares*). The proportion of initial N and initial P remaining differed between litter types and decreased in *G. africana* and *E. rhinocerotis* but increased in *W. borbonica* ($p < 0.05$ in all cases). Standard *error bars* when not visible are smaller than the *dots*

Table 3 Decomposition rates (*k*) and half-life of litter of South African fynbos and renosterveld species

Species	Vegetation type	*k* value (day^{-1})	Half-life (days)	Source
Galenia africana	Renosterveld	0.00674	101	1
Elythropappus rhinocerotis	Renosterveld	0.00222	308	1
Watsonia borbonica	Fynbos/renosterveld	0.00029	2,032	1
Leucospermum parile	Lowland fynbos	0.00080	887	2
Leucospermum parile	Lowland fynbos	0.00065	1,062	3
Pterocelastrus tricuspidatus	Strandveld	0.00051	1,366	3
Protea repens	Lowland fynbos	0.00013	5,161	4
Protea repens	Mountain fynbos	0.00018	3,778	4

Data from this study (1) and the literature (2–4)

1 this study; 2 Mitchell et al. (1986). Calculated from data on ash-free dry mass loss; 3 Witkowski (1991). Calculated from turnover time; 4 Mitchell and Coley (1987). Calculated from dry mass half-life

these differences could also be a consequence of the fact that only a few, typically proteoid species in fynbos vegetation have been investigated. Thus, it is possible that decomposition is also much more variable (i.e. with some species having half-lives similar to those we found for *G. africana* and *E. rhinocerotis*) in the typical fynbos vegetation than the few studies undertaken to date suggest.

Such an assumption also seems plausible given that decomposition was highly variable among the renosterveld species investigated here (Table 3). In fact, *G. africana* and *E. rhinocerotis* show decomposition rates within the range of shrubs and deciduous trees in other biomes (see Fig. 1 in Enríquéz et al. 1993). In contrast, the half-life of *W. borbonica* litter was more similar to the previously studied Proteid shrub species in fynbos, such as *Protea* and *Leucospermum* (Table 3), which is extremely slow compared to the decomposition rates presented in Enríquéz et al. (1993).

Our results suggest that decomposition processes in the fynbos biome are more complex and variable than indicated by previous studies, as anticipated by, e.g., Mitchell (1983) and Stock and Allsopp (1992). The results also question the previous generalisation that fire is the main factor contributing to litter breakdown and nutrient release in this biome (Mitchell et al. 1986). Although it is obvious that fire must play an important role in decomposition in some years, especially for species with long half-lives, such as the proteoids and *W. borbonica*, the considerable diversity of species and higher taxa within a given area of fynbos (e.g. Cowling et al. 1997; Cowling and Lombard 2002) indicates that biological decomposition by soil fauna and microbial communities has likely been underestimated, as earlier suggested by Marion (1982). For instance, assuming a fire interval of about 11 years, the estimated average for fynbos systems (van Wilgen 2009), the decomposition rates measured in our study would imply that that biological decomposition accounted for more than 80% of the removal of *G. africana* litter, but only about 30% of *W. borbonica*. This is, of course, a rough estimate, but it emphasises that a better understanding of decomposition in this biome requires studies relating this process to variation in plant species identity and nutrient composition within and among vegetation types. Also, differential fire frequencies and the nutrient status of soils need to be taken into account. In particular, there is a need to study the contribution from short-lived seasonal or annual plants to biological decomposition rates.

In this study, plant litter with higher nutrient contents decomposed faster (Fig. 2). Such a relation with initial nutrient content has been documented in numerous previous studies (e.g. Enríquéz et al. 1993; Sterner and Elser 2002). During decomposition, C/N and C/P ratios decreased in all litter types. This increase in litter nutrient concentration is primarily a function of respiration (carbon-use efficiency) and the degree of nutrient uptake and immobilization by decomposers, which both depend on litter quality (nutrient content) (Manzoni et al. 2008). Consequently, the increase in concentration was strongest in the nutrient poor brown *W. borbonica.* This mechanism has been well documented for N-mineralisation (Manzoni et al. 2008), but we here show an even more pronounced effect on P.

The effect of litter quality becomes even more clear when considering the total amount of nutrient remaining in the litter rather than the concentration (Fig. 4 vs. Fig. 3). In the two nutrient rich litters, nitrogen and phosphorus was mineralised and lost from the litter bags into the soil. By contrast, in the extremely nutrient poor *W. borbonica*, these elements actually accumulated in the litter bags throughout the experimental period. Hence, there was a net transportation from the surroundings into the litter bags, possibly because of fungal activity (Staaf and Berg 1982; Lindahl and Olsson 2004). Alternatively, passive transportation (leakage) of nutrients from the surrounding soil could have occurred. In the present case, the fact that *W. borbonica* litter bags actually increased in mass of organic matter during the first 65 days supports the first suggestion. In any case, it seems likely that an increased concentration of nutrients was important to initiate the delayed decomposition in this species and that the mineralised nutrients subsequently were taken up; i.e. immobilised by the decomposers. In another study of the fynbos plant *Leucospermum parile*, a slight increase in P content during the first year of decomposition was observed (Mitchell et al. 1986). The concentrations of K, Na and Mg in *W. borbonica* showed similar increases during decomposition as did N and P. By contrast, in the two litters with high decomposition rates, concentrations of K and Na decreased during the study period, probably because they are easily dissolvable. The different behaviour of C/Ca ratios was not related to mass loss.

Galenia africana contains secondary compounds that are toxic to grazers (Van der Lugt et al. 1992; Vries et al. 2005). Nevertheless, it was the most easily decomposed litter, indicating that secondary compounds may not inhibit decomposition processes, possibly because qualitative chemical defences occur in low concentrations in litter and are fairly easily decomposed or leached out of the litter (Schonholzer et al. 1998).

Plant species effects on decomposer communities have commonly been observed on the spatial scale of a few metres (e.g. Saetre and Bååth 2000; Ettema and Wardle 2002; Viketoft et al. 2005). We found no evidence for the 'home-field advantage' hypothesis among decomposer communities (e.g. Ayres et al. 2009) that litter of a species would decompose faster under bushes of the same species than when placed under bushes of another species. This holds for both the defining species of renosterveld (*E. rhinocerotis*), as well as for one of the most important indicators of disturbance in this vegetation type (*G. africana*). Thus, these decomposer communities do not seem to be adapted to the litter of a particular plant species at the scale of single shrub individuals. This is consistent with previous conclusions by Wardle (2005) and Ehrenfeld et al. (2005). By contrast, all plant litter types tended to decompose slightly faster under *G. africana* than under *E. rhinocerotis*. This could be a consequence of more suitable microclimate conditions for decomposition under *G. africana*. Another reason could be related to the fact that nutrient conditions have been suggested to increase under *G. africana* bushes (Allsopp 1999). This suggestion is supported by our finding that litter placed under *G. africana* had higher nutrient concentrations than litter placed under *E. rhinocerotis* (Online Resource, Appendix 3). Hence, all else being equal, microbial decomposers may be more active under *G. africana* resulting in a slightly higher decomposition rate.

Conclusions

Our results suggest that litter decomposition rates in the fynbos biome may be more variable than indicated by previous studies, which were confined to fynbos vegetation. There seems to be considerable variation between the renosterveld and fynbos vegetation, but also between different litter types within these vegetation types. Thus, previous generalisations regarding the key role of fire for decomposition processes in this biome may need to be revisited. Finally, our study addressed the 'home-field advantage' hypothesis among decomposer communities in renosterveld, but we did not find any evidence that these are adapted to the dominant plant species at the scale of single plant individuals.

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References

Ågren GI, Bosatta E (1996) Theoretical ecosystem ecology, understanding element cycles. Cambridge Univiversity Press, Cambridge

Allsopp N (1999) Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. Plant Ecol 142:179–187

Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N, Parton WJ, Moore JC, Wall DH (2009) Home-field advantage accelerates leaf litter decomposition in forests. Soil Biol Biochem 41:606–610

Cowling RM, Lombard AT (2002) Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. Diversity Distrib 8:163–179

Cowling RM, Richardson DM, Muster PJ (1997) Fynbos. In: Cowling RM, Richardson DM, Pierce SM (eds) The vegetation of southern Africa. Cambridge University Press, Cambridge, pp 99–130

de Deyn GB, Raaijmakers CE, van Ruijven J, Berendse F, van der Putten WH (2004) Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. Oikos 106:576–586

Donaldson J, Nänni I, Zachariades C, Kemper J (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. Cons Biol 16:1267–1276

Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant-soil system. Annu Rev Environ Resour 30:75–115

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phophorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142

Enríquéz S, Duarte CM, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94:457–471

Ettema CH, Wardle DA (2002) Spatial soil ecology. Trends Ecol Evol 17:177–183

Hobbie SE, Vitousek PM (2000) Nutrient limitation of decomposition in Hawaiian forests. Ecology 81:1867–1877

Kemper J, Cowling RM, Richardson DM (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biol Cons 90:103–111

Lindahl BD, Olsson S (2004) Fungal translocation—creating and responding to environmental heterogeneity. Mycologist 18:79–88

Linder HP (2003) The radiation of the Cape flora, southern Africa. Biol Rev 78:597–638

Loreau M (1998) Biodiversity and ecosystem functioning: a mechanistic model. Proc Natl Acad Sci USA 95:5632–5636

Manning J (2007) Field guide to fynbos. Struik, Cape Town

Manzoni S, Jackson RB, Trofymow JA, Porporato A (2008) The global stoichiometry of litter nitrogen mineralization. Science 321:684–686

Marion GM (1982) Nutrient mineralisation processes in mediterranean-type ecosystems. In: Conrad CE, Oechel WC (eds) Proceedings of the symposium on dynamics and management of mediterranean-type ecosystems. San Diego, California, pp 313–320

Mitchell DT (1983) Section 3, nutrient cycling. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds) Mediterranean type ecosystems. The role of nutrients. Ecological studies 43. Springer, Berlin, pp 177–178

Mitchell DT, Coley PGF (1987) Litter production and decompositions from shrubs of *Protea repens* growing in sand plain lowland and mountain fynbos, south-western Cape. S Afr J Bot 53:25–31

Mitchell DT, Coley PGF, Webb S, Allsopp N (1986) Litter fall and decomposition processes in the coastal fynbos vegetation, south-western Cape, South Africa. J Ecol 74:977–993

Mucina L, Rutherford MC (eds) (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331

Osler GHR, Sommerkorn M (2007) Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88:1611–1621

Proksch P, Proksch M, Rundel PW, Rodriguez W (1982) Ecological significance of the chemistry of the leaf resin of *Elytropappus rhinocerotis*. Biochem Syst Ecol 10:49–53

Richards MB, Stock WD, Cowling RM (1997) Soil nutrient dynamics and community boundaries in the fynbos vegetation of South Africa. Plant Ecol 130:143–153

Rouget M, Richardson DM, Cowling RM, Lloyd JW, Lombard AT (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. Biol Cons 112:63–85

Saetre P, Bååth E (2000) Spatial variation and patterns of soil microbial community structure in a mixed spruce-birch stand. Soil Biol Biochem 32:909–917

Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195:260–262

Schonholzer F, Kohli L, Hahn D, Daniel O, Goez C, Zeyer J (1998) Effects of decomposition of leaves on bacterial biomass and on palatability to *Lumbricus terrestris* L. Soil Biol Biochem 30:1805–1813

Simons L, Allsopp N (2007) Rehabilitation of rangelands in Paulshoek, Namaqualand: understanding vegetation change using biophysical manipulations. J Arid Env 70:755–766

Staaf H, Berg B (1982) Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long term decomposition in a Scots pine forest II. Can J of Bot 60:1561–1568

Sterner RW, Elser JJ (2002) Ecological stoichiometry. Princeton University Press, Princeton

Stock WD, Allsopp N (1992) Functional perspective of ecosystems. In: Cowling RM (ed) The ecology of fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town, pp 241–259

Stock WD, Lewis OAM (1986) Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. J Ecol 74:317–328

Sudderth EA, Stinson KA, Bazzaz FA (2005) Host-specific aphid population responses to elevated CO2 and increased N availability. Glob Chang Biol 11:1997–2008

Thuiller W, Midgley GF, Rouget M, Cowling RM (2006) Predicting patterns of plant species richness in megadiverse South Africa. Ecography 29:733–744

Todd SW, Hoffmann MT (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecol 142:169–178

Usher MB, Booth RG, Sparkes KE (1982) A review of progress in understanding the organization of communities of soil arthropods. Pedobiologia 23:126–144

Van der Lugt JJ, Schultz RA, Fourie N, Hon LJ, Jordaan P, Labuschagne L (1992) *Galenia africana* L. poisoning in sheep and goats: hepatic and cardiac changes. J Vet Res 59:323–333

Van Wilgen BW (2009) The evolution of fire and invasive alien plant management practices in fynbos. S Afr J Sci 105:335–342

van Wyk BE, van Oudtshoorn B, Gericke N (2000) Medicinal plants of South Africa, 2nd edn. Briza, Pretoria

Viketoft M, Sohlenius B, Palmborg C, Huss-Danell K, Bengtsson J (2005) Plant species effects on soil nematode communities in experimental grasslands. Appl Soil Ecol 30:90–103

Viketoft M, Bengtsson J, Sohlenius B, Berg MP, Petchey O, Palmborg C, Huss-Danell K (2009) Long-term effects of plant diversity and composition on soil nematode communities in grasslands. Ecology 90:90–99

Vitousek PM (2004) Nutrient cycling and limitation: Hawaii as a model system. Princeton University Press, Princeton

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87–115

Vries FA, El Bitar H, Green LR, Klaasen JA, Mabulesa WT, Bodo B, Johnson Q (2005) An antifungal active extract from the aerial parts of *Galenia africana*. In: Midiwo JO, Yenesew A, Derese S (eds) 11th NAPRECA symposium book of proceedings, Antananarivo, Madagascar, 2005. Napreca, Nairobi, Kenya, pp 123–131. (http://www.napreca.net)

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton

Wardle DA (2005) How plant communities influence decomposer communities. In: Bardgett RD, Usher MB, Hopkins DW (eds) Biological diversity and function in soils. Cambridge University Press, Cambridge, pp 119–138

Whitham TG, Young WP, Martinsen GD, Gehring CA, Schweitzer JA, Shuster SM, Wimp GM et al (2003) Community and ecosystem genetics: a consequence of the extended phenotype. Ecology 84:559–573

Witkowski ETF (1989) Effects of nutrient additions on litter production and nutrient return in a nutrient-poor Cape fynbos ecosystem. Plant Soil 117:227–235

Witkowski ETF (1991) Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. J Appl Ecol 28:1–15

AUTHOR: C. JANION

SPRINGTAILS

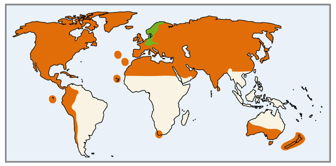
Class Collembola

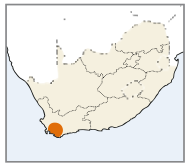
Springtails are primitive, wingless invertebrates (Apterygotes) and among the most abundant and widespread organisms in the world, being especially common in soil. They are best recognised by their unique forked jumping organ, or furca, folded under the abdomen, and the 'ventral tube', an abdominal organ used for water balance. There are more than 7 000 species. Although they resemble insects, some scientists argue that they are more closely related to crustaceans.

Clover springtail

Sminthurus viridis

Group: Symphypleona: Sminthuridae





Habitat: Terrestrial, plant-feeding. Occurs in a wide variety of habitats, including grasslands and field crops, such as clover. **Identification and biology:** Typical spherical body shape, 2–4 mm long, usually green or yellowish-brown; depending on environmental conditions can produce several generations per year. Eggs laid in soil. **Introduction and spread:** Origin likely Europe, now widely spread in temperate parts of the world, including Australia, where it is a pest of legumes and cereals and is known as the 'lucerne flea'. Probably introduced to South Africa from Australia. **Impacts:** Can cause damage to leguminous crops such as alfalfa (lucerne). Green leaves of crops are frequently eaten, and seedling death may occur with heavy infestations. **Control:** Systemic and contact insecticides have been used. The predatory Pasture snout mite (*Bdellodes lapidaria)* was released in Caledon in 1963 as a biocontrol agent.

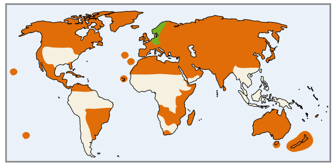
Key reference: Wallace, M.M.H. 1974. Present and probable world distribution of *Sminthurus viridis* and prospects for its biological control. *Pedobiologia*, 14:238-243.

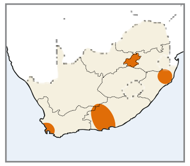
C. Janion

Marsh springtail

Isotomurus palustris

Group: Entomobryomorpha
Isotomidae





Habitat: Terrestrial, in wet habitats. **Identification and biology:** Up to 2.5 mm in length, with a yellow-brown colour pattern and darker central dorsal stripe. Long, thin hairs on the dorsal side of abdomen on the second to fourth abdominal segments are characteristic of the genus. **Introduction and spread:** A northern European species that has spread globally and is now one of the most frequently recorded species, with a cosmopolitan distribution in temperate areas. Found in damp habitats associated with standing water. **Impacts:** Causes plant damage when occurring in large numbers, but effects on plants usually secondary as feeds mostly on decaying plant material. **Control:** None recorded, but have been used in toxicity tests.

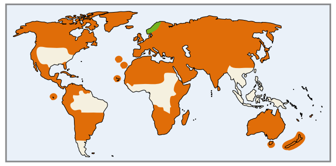
Key reference: Fjellberg, A. 2007. The Collembola of Fennoscandia and Denmark, Part II. Entomobryomorpha and Symphypleona. *Fauna Entomologica Scandinavica* Vol. 43. Leiden: Brill Academic Publishers.

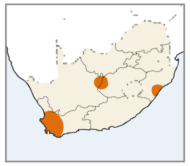
C. Janion

Mushroom springtail

Hypogastrura manubrialis

Group: Poduromorpha:
Hypogastruridae





Habitat: Terrestrial, usually in upper soil and litter layer. **Identification and biology:** Up to 1.5 mm in length, colour grey to reddish-blue. **Introduction and spread:** Originally from northern Europe, now cosmopolitan in distribution, including scattered localities in South Africa. Usually found in disturbed areas or near human dwellings. **Impacts:** Considered a pest of mushrooms as outbreaks have occurred on mushroom farms in Europe. However, this is no longer a problem as soil sterilisation is now standard procedure among commercial mushroom growers. Found in manure in glasshouses in Australia, but no damage recorded. **Control:** Measures against outbreaks include disinfection during preparation of mushroom beds and use of sterile manure. Known to have a high resistance to insecticides.

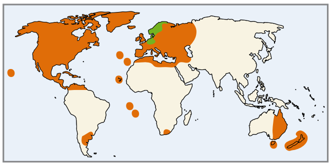
Key reference: Fjellberg, A. 1998. The Collembola of Fennoscandia and Denmark, Part I. Poduromorpha. *Fauna Entomologica Scandinavica* Vol. 35. Leiden: Brill Academic Publishers.

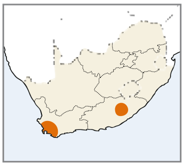
C. Janion

Moss springtail

Neanura muscorum

Group: Poduromorpha: Neanuridae



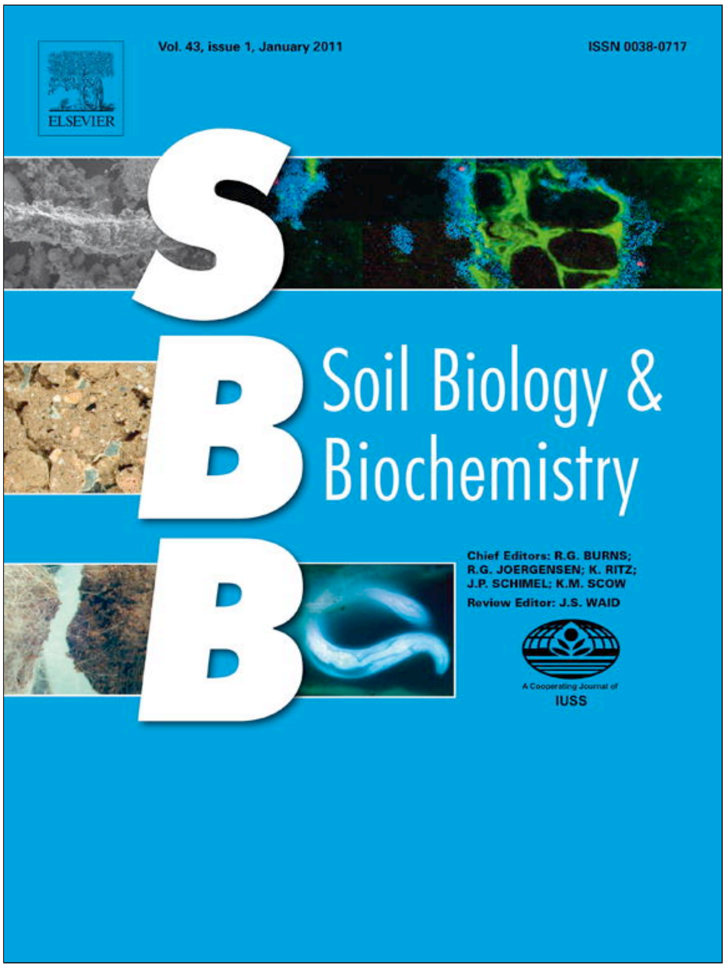


Habitat: Terrestrial, in a wide variety of habitats from coastal to alpine, usually in litter and under rotting wood. **Identification and biology:** Size up to 3.5 mm, colour bluish-grey to lilac. Body has a distinctive warty appearance, hair long and spiny and three eyes on each side of head. Aromatic substances secreted may play a role as defence against predators. Mostly parthenogenetic, the females laying unfertilised eggs that develop into viable offspring, but sexual forms are found. Like all Collembola, they moult throughout their adult life. **Introduction and spread:** A northern European species now found in most temperate regions of the world. Localised in the Eastern and Western Cape provinces of South Africa. **Impacts:** None known, and given their small size and benign feeding habits unlikely to be harmful. **Control:** None recorded.

Key reference: Coates, T.J. 1986. The Collembola of South Africa. 1. The genus *Neanura*. *Journal of the Entomological Society of Southern Africa*, 31:185-195.

C. Janion

C. Janion



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Litter decomposition in fynbos vegetation, South Africa

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ABSTRACT

The Western Cape of South Africa is characterized by the hyperdiverse vegetation of the Fynbos biome. Typical fynbos vegetation is a fire-adapted sclerophyllous Mediterranean-type ecosystem on poor, sandy or stony soils. It is characterized by plants with low nutrient content producing slowly decomposing litter. Fire is recognized as a major factor for carbon and nutrient cycling in this vegetation type. However, knowledge of biological decomposition processes in this biome is limited. We used litter-bags to measure mass loss and changes in chemical composition in litter from three species representing characteristic taxa in fynbos, a *Protea exima* hybrid, *Erica multumbellifera*, and *Restio multiflorus*, during approximately 180 days. In addition, we used a standard litter of a species with high nutrient content, *Galenia africana*, and a mixture of *Protea* and *Erica*. We compare our results with a previous study from renosterveld including the geophyte *Watsonia borbonica*, which occurs in both vegetation types and occurs commonly in the study area. We found that decomposition rate among the true fynbos plant species *P. exima*, *E. multumbellifera*, *R. multiflorus* and *W. borbonica* varied almost eight-fold. Litter decomposition was strongly correlated to litter stoichiometry, i.e. C/N and C/P-ratios. Most litters accumulated one or several nutrients during the study period. The mixture of litters decomposed faster than expected from the results of each litter separately. Our study indicates that biological decomposition may be more important for carbon and nutrient cycling in fynbos than previously thought. These results are in accordance with recent studies showing large variation in plant litter quality within vegetation types and biomes. Such large variation in litter quality and decomposition rate suggests that some generalisations about ecosystem processes in the fynbos may need reevaluation.

1. Introduction

Decomposition of plant litter is affected by variation in the substrate quality of litter, environmental conditions, and the composition of decomposer communities (Parton et al., 2007; Osler and Sommerkorn, 2007; Cornwell et al., 2008; Jonsson and Wardle, 2008; Carrillo et al., 2011). In contrast to what has previously been thought, recent studies have shown that decomposition rates appear to be more strongly affected by plant quality than by variation caused by environmental factors. Cornwell et al. (2008) found a 10.5-fold average difference in species decomposition rates within climate zones, which is twice as large as the variation in decomposition rate of common substrates attributable to different climate conditions. Large variation in leaf litter quality or decomposition among plant taxa has also been found locally within vegetation types and climate zones (e.g. Hättenschwiler et al., 2008; Kazakou et al., 2009; Wardle et al., 2009; Bengtsson et al., 2011). This variation in decomposition rates among plant species has been attributed to variation in ecological traits, such as leaf nutrient composition, associated with different plant strategies and phylogenetic groups (Cornwell et al., 2008). The dominant role of plant leaf and litter traits implies that previous generalisations about decomposition processes may need reevaluation in a variety of vegetation types and climatic regions.

The Western Cape of South Africa is characterized by the hyperdiverse vegetation of the Fynbos biome (Cowling and Lombard, 2002; Linder, 2003; Mucina and Rutherford, 2006). Typical fynbos vegetation is fire-adapted, sclerophyllous and occurs on poor, sandy or stony soils (Mucina and Rutherford, 2006). It is characterized by Proteaceae and Ericaceae shrubs, and the reed-like Restionaceae, but it also contains a diversity of geophytes, and in drier areas short-lived annuals (Manning, 2007). Several other vegetation types are found in the Fynbos biome, one of which is the renosterveld, which occurs on richer soils and is also fire-prone (Rebelo et al., 2006). In a previous

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study, we found a 20-fold difference in decomposition rate between three representative plant species from renosterveld (Bengtsson et al., 2011). Here we extend these results to the true fynbos vegetation. Biological decomposition of typical fynbos plant species has previously been suggested to be very low, and carbon and nutrient dynamics dependent upon the periodic fires characteristic of fynbos (Mitchell et al., 1986; Witkowski, 1991; Stock and Allsopp, 1992). However, the considerable diversity of plant species and functional types within a given area of fynbos (e.g. Cowling et al., 1997; Cowling and Lombard, 2002) suggests that plant litter quality and hence biological decomposition may vary between functional types of plants within sites, in a way similar to that found in renosterveld (Bengtsson et al., 2011). As a consequence, biological decomposition by soil fauna and microbial communities may have been underestimated and deserve more attention. For example, nutrient turnover of plant litter with higher nutrient content may be much faster and less dependent on fire than is the case for the previously studied nutrient-poor species in the Proteaceae and Restionaceae (e.g. Mitchell et al., 1986; Mitchell and Coley, 1987; Witkowski, 1991).

In this paper, we examine whether species-specific differences in first-year decomposition rates of three representatives of major fynbos taxa, as measured by organic matter mass loss, are related to their nutrient content (carbon-to-nutrient ratios), as an indicator of plant litter quality. The species we studied represent the natural range of litter nutrient content and life forms in this biome (see below and van Wilgen and le Maitre, 1981; Mucina and Rutherford, 2006). We also investigate changes in nutrient content of the different plant litters during decomposition, and whether litter from different plant species decomposes faster when placed in vegetation dominated by their own functional type rather than vegetation dominated by another functional type, i.e. if a home field advantage (Ayres et al., 2009) exists. We compare these results with a standard litter used previously (*Galenia africana*) in our investigations of decomposition in renosterveld (Bengtsson et al., 2011). Finally, because plant litter seldomly occurs as a monoculture in the diverse fynbos vegetation, we determine whether a mixture of litters from two characteristic fynbos taxa with different quality decomposes at rates different to those expected from the single species litters. Increased decomposition would be expected if, for example, nutrients such as nitrogen from the more nutrient-rich litter is used by decomposers utilizing the nutrient-poor litter (e.g. Gartner and Cardon, 2004).

2. Materials and methods

2.1. Study site, plant species and sampling methods

The study was carried out from mid-March to mid-September 2008, during the South African winter, using methods described in detail in Bengtsson et al. (2011). This part of South Africa has a Mediterranean climate with cool, wet winters and hot, dry summers. While studying springtail (Collembola) abundance and diversity, we also recorded mass loss and changes in chemical composition of litter of four plant species placed in litter-bags. Three of the species represented three major components of the fynbos vegetation type in the Western Cape, South Africa, viz. Ericaceae, Proteaceae and Restionaceae. In addition we used a shrub species characteristic of disturbed areas, *G. africana*, and a litter mixture of the Ericaceae and Proteaceae species.

The four plant species used were: (1) The hybrid *Protea exima* × *Protea susannae*, var. 'silva' and 'cardinal'; (2) *Erica multumbellifera*. For conservation reasons, as the study was carried out in a nature reserve, and to obtain litter of standard quality, *E. multumbellifera* was collected from Heuningkloof farm in Kleinmond, while the *Protea* was obtained from Flower Valley Farm, Gansbaai. The plants from which we derived the litter may have received some fertilizer in a previous growing season, although no clear information on this was available; (3) *Restio multiflorus*, which was collected from a field site on Whitewater Lodge estate close to Stanford; (4) *G. africana* (Aizoaceae), which is a common shrub in the Western Cape, and an indicator of disturbance such as overgrazing (Allsopp, 1999; Todd and Hoffmann, 1999). It is toxic to sheep and goats (Van der Lugt et al., 1992; Vries et al., 2005) and has been argued to enrich soils under its canopy with nitrogen and phosphorus (Allsopp, 1999; Simons and Allsopp, 2007). This species was collected from an overgrazed rangeland west of the Paarl mountain. *G. africana* is usually not found in true fynbos, but we used it for two reasons: First, we wanted to have a standard litter to be able to compare decomposition across sites and between years, and second because we wanted to include a nutrient-rich litter in the fynbos study, in a similar way as done previously in renosterveld (Bengtsson et al., 2011). All litters were obtained from live plants at the end of the dry season, and hence partly senescent; for practical reasons it was not possible to gather litter by litterfall traps over an extended period.

The study site consisted of three plots in the Jonkershoek Nature Reserve close to Stellenbosch, South Africa (S33° 58.809′, E18° 56.862′). All plots were situated in natural fynbos vegetation, but in different vegetation types, viz. proteoid, ericoid or restioid, respectively. The proteoid plot was dominated by *Protea nitida*, the ericoid by *Erica hirta*, *and* the restioid plot by *Elegia capensis*. In each plot we selected 10 shrubs or tufts along an L-shaped transect with approximately 10 m between each shrub. Under each shrub (tuft) 5 litter-bag traps filled with different litters were placed – four with single species and one with the mixture. The traps were placed in the soil with the top of the trap at ground level, within 3–4 cm from each other and less than 40 cm from the shrub base on the south-west to south-east side to minimise sun exposure.

The litter-bags were individually numbered cylindrical plastic containers with a height of 4 cm and a diameter of 7.5 cm (Bengtsson et al., 2011). The bottom consisted of a steel net with mesh size 0.5 mm. The traps had a removable lid with 1.6 mm mesh size to allow animals to enter the trap. In the laboratory they were filled with well-mixed air-dried litter up to approx. 3.5 cm, which had been weighed to nearest 0.1 mg on an electronic balance (FA304T, Avery Berkel, Fairmont, USA). The litter was not compressed and was allowed to maintain its normal volume and density.

The litter-bag traps were placed in the field on 10 March 2008 and were collected on 8 or 17 September 2008, i.e. after 182 and 191 days respectively. Trap sets 1–5 from each of the sites were sampled on the first date, and sets 6–10 on the second date. This was done for extraction capacity reasons, because soil fauna was also collected. The traps were brought into the laboratory and treated as in Bengtsson et al. (2011). Total C and N concentrations were determined using a Carlo-Erba NA 1500 Elemental Analyzer, while P, K, Na, Mg and Ca were measured by Inductively Coupled Plasma Atomic Spectroscopy (see Bengtsson et al., 2011). Two samples were accidentally mislabelled during the chemical analyses and therefore excluded from the data set.

2.2. Statistics

We measured mass loss as the loss of organic matter from each litter-bag. Mass loss was determined using ash free dry weight measurements. To compare our results with other studies, we also calculated the decomposition constant k assuming the exponential decomposition model (Olson, 1963), i.e. $W_t = W_0 \, e^{-kt}$, where W_0 is the mass of organic matter at the start of the experiment and W_t is the mass of organic matter at the end ($t = 182$ or 191 days). The constant k has unit day^{-1} and was calculated for each litter-bag.

Carbon-to-nutrient ratios were calculated on a weight basis using the data from the chemical analyses. All variables were square-root-transformed before statistical analysis.

The data were analysed with a split-plot analysis of variance, with Vegetation Type (Proteoid, Ericaceaous or Restioid) as whole plots, with the error term Vegetation Type*Shrub ID, and Litter Type (5 levels) as the split-plot factor with the residual as error term. The interaction between Litter Type and Vegetation Type was included in all models, with the residual as error term. The approximately balanced design of the present study ($n = 29$ or 30 in all litter treatments) means that the split-plot model gives essentially the same results as a mixed model (GLMM). The analyses were undertaken with the SuperAnova program for Macintosh (Abacus inc., 1918 Bonita Ave. Berkeley, CA). To examine relationships between mass loss and C/nutrient ratios in the original litter, we used Microsoft Excel spreadsheet functions.

2.3. Analysis of decomposition of mixed vs. single species litter

To determine whether mixed *Protea–Erica* litter had higher mass loss than expected from the mass loss from the two single litters, we employed a randomization test using Microsoft Excel spreadsheets. The procedure assumed that there was no effect of vegetation type on decomposition, an assumption that is fulfilled in our case (Table 2a). From the 29 single litter litter-bags of each species we randomly chose 29 combinations of mass loss values, and calculated the expected mass loss in the mixed litter-bags based on the average initial proportion of *Erica* litter in the mixed litter-bags, which was 55.7%. From these values we calculated the expected mean mass loss and its standard deviation. The expected and the observed mass loss in mixed litter-bags was compared using a *t*-test with $df = 2*(29 - 1) = 56$ and $t_{0.05,56} = 2.01$ (following Sokal and Rohlf, 1991). It was noted if the difference between expected and observed mass loss was significant at the $p = 0.05$ level. This procedure was repeated 100 times, each time with a new set of randomly selected combinations of single litters, and the proportion of significant *t*-tests was used as an indicator whether mass loss was higher from mixed litters than expected from single species litter-bags. In our case, there were no instances when the *t*-test was non-significant, so we stopped the randomization test after 100 iterations.

3. Results

Mass loss during the six month period (≈185 days) differed almost 7-fold between the four species (Table 1). Litter type (including the mixture) explained most of the variation in decomposition (Table 2). All differences between single species litters were significant (Tukey–Kramer tests, $p < 0.05$). There was no significant effect of vegetation type or the litter type*vegetation type interaction (Table 2a). Hence we found no support for different litter types decomposing faster when placed in vegetation dominated by their own plant functional type.

The standard litter of the non-fynbos species *G. africana* decomposed the quickest, losing almost 70% of its organic matter mass during the study period. The *Protea* hybrid decomposed fastest of the fynbos plants, losing approximately 35% of the initial mass. *R. multiflorus* decomposed the slowest, with only about 10% of the initial mass disappearing, while *E. multumbellifera* was intermediate with a mass loss of 25% (Table 1). The decomposition constant *k* showed similar variation, with an almost 4-fold difference between the three true fynbos species (Fig. 1; black dots). These values correspond to litter half-lives (calculated as $0.693{*}k^{-1}$; Olson, 1963) of 108, 297, 462 and 1136 days for *Galenia*, *Protea*, *Erica* and *Restio*, respectively.

Decomposition was 14.6% faster in the mixed *Protea*/*Erica* litter than expected from the two single species litters (Table 1; Fig. 1). This difference is statistically significant, as shown by the randomization test. We found a significant difference between the observed and expected mass loss (as examined with *t*-tests) in all of the 100 randomizations. In the split-plot ANOVA, mass loss of the mixed litter was significantly higher than that of *Erica* litter (Table 1; Tukey–Kramer test, $p < 0.05$), but did not differ significantly from the slightly faster decomposing *Protea* litter (Table 1; Tukey–Kramer test, ns).

Combining the present data with previous results from renosterveld (Bengtsson et al., 2011), a strong negative relationship was found between decomposition rate *k* and initial C/N-ratio (Fig. 1), which was well described by the equation $k = 0.0095\,e^{-0.0225\,(\text{C/N-ratio})}$ ($r^2 = 0.87$). Similar negative relationships were found between *k* and initial C/P ratio, as well as for C/Mg and C/Na. However, it was not meaningful to calculate separate relationships between *k* and the other nutrients because the concentrations of different nutrients and consequently C/nutrient ratios in the initial litter were highly collinear (e.g. N and P content, $r = 0.987$, $n = 8$, $p < 0.001$; Appendix 3 for other nutrients). Because of this high collinearity it is not possible to examine the relative importance of the different nutrients for decomposition rate.

Significant effects were found of plant litter type on carbon-to-nutrient ratios at the end of the study (Tables 2 and 3; Appendix 1 and 2). C/N-ratios differed significantly between all litters (Tukey–Kramer tests, $p < 0.05$) while C/P-ratios did not differ

Table 1
Mass loss (proportion organic matter mass lost from litter-bags during ≈185 days) of plant litter of four species, the standard litter *Galenia africana*, three representatives of major components of fynbos vegetation (*Erica*, *Protea* and *Restio*), and the mixture of *Protea* and *Erica*. See Fig. 1 for *k*-values. $n = 30$ (29 for *Erica* and *Protea*). *Mass loss data for the species *Watsonia borbonica* placed in the renosterveld for 182 days, from Bengtsson et al. (2011), has been added for comparison but is not included in the statistical tests.

Species	Mass loss	SE
Galenia africana	0.6904	0.00792
Erica multumbellifera	0.2420	0.00810
Protea exima × susannae	0.3503	0.00810
Mixture *Protea/Erica*	0.3234	0.00792
Restio multiflorus	0.1072	0.00792
*Watsonia borbonica**	0.0950	0.00952

All differences between litters were significant (Tukey–Kramer tests $p < 0.05$) except the difference between *Protea* and the mixture. The effects of vegetation type and the interaction between litter type and vegetation were not significant (See Table 2 for statistics).

Table 2
Results from split-plot ANOVAs of effects of plant litter type and vegetation type on (a) mass loss and (b) final litter C/N-ratio. The dependent variables were square-root-transformed prior to analysis. Vegetation type was used as whole plot, with the error term Vegetation Type*Shrub ID, while Litter Type was the split-plot factor with the residual as error term.

Factor	df	SS	*F*	*p* <
(a) Mass loss				
Vegetation type	2	0.02213	2.10	0.135 ns
Vegetation type*Shrub ID	27	0.13816		
Litter type	4	4.10127	559.1	0.0001
Litter type*Vegetation Type	8	0.01838	1.253	0.28 ns
Residual	106	0.19440		
(b) Final C/N-ratio				
Vegetation type	2	2.601	5.099	0.013
Vegetation type*Shrub ID	27	6.885		
Litter type	4	545.4	1120	0.0001
Litter type*Vegetation Type	8	2.544	2.611	0.012
Residual	106	12.91		

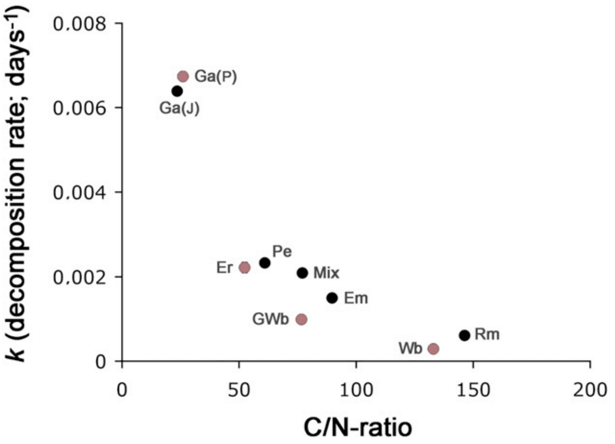

Fig. 1. Relationship between initial litter quality, measured as C/N-ratio, and decomposition rate k in litters from the experiment in fynbos vegetation in Jonkershoek (this study; black dots; J) and in litters from renosterveld near Piketberg, South Africa (Bengtsson et al., 2011; red dots; P). Standard errors of the means are smaller than the size of the dots. Litters are the standard litter of *Galenia africana*, Ga(J) and Ga(P), *Elytropappus rhinocerotis*, Er (P), *Protea exima* × *susannae*, Pe (J), green *Watsonia borbonica*, GWb (P), mixture of Pe and Em (J), *Erica multumbellifera*, Em (J), brown *W. borbonica* leaves Wb (P), and *Restio multiflorus*, Rm (J). The exponentially decreasing relationship is described by the equation $k = 0.0095\ e^{-0.0225\ (C/N-ratio)}$ ($r^2 = 0.87$). Data for green Watsonia (GWb) from J. Bengtsson, C. Janion, S.L. Chown, H.P. Leinaas (unpublished). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significantly between *Protea*, *Erica* and the mixture. Both *Galenia* and *Restio* differed from all the other species. C/N-ratios had decreased in all litters, while C/P-ratio showed a different pattern, with decreases in the *Protea*, mixture and *Restio* but no clear changes in *Galenia* and *Erica* litter (Table 3; this table also contains nutrient concentrations of N and P, which changed as a consequence of the changes in C/N and C/P-ratios). There was a significant effect of vegetation type on final C/N-ratio, which became slightly lower at the *Protea* site than at the two other sites. Nevertheless, litter type was by far the most important factor explaining variation in this ratio, F-values differing more than 200-fold (Table 2). The total amount of nitrogen at the end of the study period had increased by 7–31 % in all litters except *Galenia*, from which 64% of the N had been lost from the litter-bags during decomposition. By contrast, the total amount of P had increased only in *Restio* litter-bags, and there by almost 100%.

Final C/Ca and C/Mg-ratios differed significantly between all litters (Tukey–Kramer tests, $p < 0.05$), while C/K and C/Na mainly differed between *Galenia* and the other species, but also between *Erica* and *Restio*. C/K and C/Na-ratios showed large increases over time in all litters. In contrast, C/Mg-ratio increased in *Galenia* but decreased in the other litters, and C/Ca decreased in all litters (Appendix 1 and 2). The other nutrients than N and P had usually been lost from all litter-bags, with the exception of Ca and Mg in the *Restio* litter-bags.

4. Discussion

Many characteristic plant species of the fynbos decompose slowly (Stock and Allsopp, 1992). Indeed, earlier decomposition studies from the fynbos found low decomposition rates (k-values<0.001 day^{-1}) and low nutrient content of plants (usually C/N > 80 and C/P > 1000; Mitchell et al., 1986; Mitchell and Coley, 1987; Witkowski, 1991). By contrast, recent studies have indicated large differences in decomposition rate between plant species within vegetation types and climatic regions (biomes) (e.g. Cornwell et al., 2008; Kazakou et al., 2009; Wardle et al., 2009; Bengtsson et al., 2011). Several of the plant species we used had both higher nutrient content and faster decomposition rates than those in previous studies of decomposition in fynbos. Thus our studies show a substantially wider range in decomposition rates of plants from the Fynbos biome than previous studies have suggested (references above; Bengtsson et al., 2011). Although some of the differences between our study and previous ones may be due to the fact that we collected *Protea* and *Erica* leaf litter at a nursery, our results provide evidence for substantial variation in decomposition rates within the fynbos vegetation type, and differ from previous results showing generally slow decomposition rates in fynbos. In particular, if we include the decomposition rate of *Watsonia borbonica* from Bengtsson et al. (2011), which is a species occurring in both fynbos and renosterveld, the difference between fynbos plants found by us is almost 8-fold (k-values from 0.0003 to 0.0023 day^{-1}) (Note: This comparison is justified because the decomposition rate of the standard litter *G. africana* was so similar between the years and sites; Fig. 1). Nutrient levels in fynbos plants have been found to vary both among plant species and with soil conditions (van Wilgen and le Maitre, 1981). Our study spans the range of nutrient concentrations and life forms included in previous studies, and can hence be considered representative in a general sense. For example, recalculated values of C/N-ratios derived from van Wilgen and le Maitre (1981, Table 2) vary 3.6-fold, and the species studied by us are distributed over most of this range. Nonetheless, it is clear that further studies on a wider range of species and sites are needed to assess the degree to which decomposition rates vary in the Fynbos biome. The large variation in decomposition rate among species from fynbos vegetation found by us, as well as the large variation in fynbos plant nutrient concentrations found by van Wilgen and le Maitre (1981), suggests that previous generalisations about decomposition processes in the Fynbos biome may need reconsideration. It also highlights the importance of understanding the ways in which plant leaf and litter traits result in different rates of decomposition, based on an understanding of plant strategies and plant functional types (Lavorel and Garnier, 2002; Cornwell et al., 2008).

Table 3
Initial and final C/N and C/P-ratios, and N and P concentrations as % of organic matter, in four plant litter types and a mixture of *Protea* and *Erica* after ≈ 185 days. The initial litter was well-mixed, while for final values ± SE represent the variation between litter-bags. See Table 1 for n-values and species names, p-values refer to an overall difference in C/nutrient ratios between plant litters after 185 days (Table 2 and Appendix 2).

Variable	Litter type					$p <$
	Galenia	*Erica*	*Protea*	Mixture	*Restio*	
Initial C/N	23.6	89.7	61.0	77.0	146.4	
% N	2.12	0.557	0.820	0.649	0.342	
Final C/N	21.0 ± 1.16	66.5 ± 1.19	34.7 ± 1.19	46.5 ± 1.16	103.7 ± 1.16	0.001
% N	2.41 ± 0.057	0.76 ± 0.012	1.44 ± 0.021	1.08 ± 0.008	0.49 ± 0.015	
Initial C/P	295.5	1390.9	1274.6	1339.4	6956.5	
% P	0.169	0.0359	0.0392	0.0373	0.00719	
Final C/P	326.3 ± 96.0	1237 ± 98.2	1057 ± 98.2	1139 ± 96.0	3682 ± 96.0	0.001
% P	0.164 ± 0.0087	0.041 ± 0.0009	0.047 ± 0.0111	0.044 ± 0.0010	0.016 ± 0.0014	

A strong relationship was found here between plant stoichiometry, i.e. C/N or C/P-ratio, and decomposition rate during the first-year wet season in our combined data (Fig. 1). Whether decomposition rates are best related to nutrient concentrations in the litter, environmental conditions, or the carbon fractions in the litter has been the subject of much discussion (e.g. Enríquéz et al., 1993; Aerts, 1997; Joffre and Ågren, 2001). The meta-analysis of Cornwell et al. (2008) suggested that litter nutrient content as well as carbon fractions are important for explaining variation in decomposition rate, and that the role of environmental conditions related to climate may have been overemphasised relative to plant traits. In the fynbos, nutrient limitation of plant growth is pervasive, although it is unclear which nutrients are most limiting (e.g. Witkowski, 1989; Richards et al., 1997). In any case, until more detailed studies are carried out it seems reasonable to use a measure of nutrient content, e.g. C/N-ratio, as an indicator of decomposition rate in this biome. Hence, the high diversity of species in fynbos may lead to a larger variation of decomposition rates than previously thought.

The mixed litter decomposed faster than expected from the single *Protea* and *Erica* litters. Although by no means ubiquitous, increased decomposition of litter mixtures has often been observed (Gartner and Cardon, 2004; Chapman and Koch, 2007; Jonsson and Wardle, 2008; Wardle et al., 2009); approximately 65% of the studies reviewed by Gartner and Cardon (2004) found this pattern. One possible mechanism for such an effect is the movement of nutrients among litters, with the higher quality litter stimulating the decomposition of the lower quality one, either by biological processes or by leaching (Gartner and Cardon, 2004). For example, nitrogen-limited decomposer fungi may use nitrogen from the more nutrient-rich *Protea* litter when acquiring energy from the *Erica* litter. The observation that mixing of litter may increase decomposition suggests that interactions between co-occurring litters may need to be taken into account when examining soil biological processes in fynbos.

To conclude, our studies from fynbos and renosterveld in the Fynbos biome in South Africa found 8- to 20-fold differences, respectively, in first-year decomposition rates between plant species representing several important taxa and functional types in these vegetation types (this study, Bengtsson et al., 2011). Both vegetation types are fire-prone, with fire intervals of 10–20 years in natural fynbos (on average 11 years; van Wilgen, 2009). Hence fires are clearly important for ecosystem processes in this biome, as shown by previous authors (e.g. Stock and Allsopp, 1992). However, the observed variation in litter quality and decomposition rates found in the present study (see also van Wilgen and le Maitre, 1981) suggests that biological decomposition may still be important for carbon and nutrient cycling between fire events. Biological decomposition is especially likely for plants with higher nutrient contents, such as *G. africana*, renosterbos *Elytropappus rhinocerotis* and the *Protea* species used here, which had litter half-lives of less than one year. Biological carbon and nutrient cycling may be most important in the years immediately after fires, when fynbos vegetation shows many adaptations that result in rapid regrowth and recovery after fire (e.g. Richardson and van Wilgen, 1992) and nutrient levels in the soil are likely to be higher (Stock and Lewis, 1986). Long-term studies examining a larger set of species during succession after fire are needed for a better understanding of the relative roles of fire and biological decomposition as well as other ecosystem processes in this biome.

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Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2011.11.023.

References

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439–449.

Allsopp, N., 1999. Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. Plant Ecology 142, 179–187.

Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochememistry 41, 606–610.

Bengtsson, J., Janion, C., Chown, S.L., Leinaas, H.P., 2011. Variation in decomposition rates in the Fynbos biome, South Africa: the role of plant species and plant stoichiometry. Oecologia 165, 225–235.

Carrillo, Y., Ball, B.A., Bradford, M.A., Jordan, C.F., Molina, M., 2011. Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil. Soil Biology and Biochemistry 43, 1440–1449.

Chapman, S.K., Koch, G.W., 2007. What type of diversity yields synergy during mixed litter decomposition in a natural forest ecosystem? Plant and Soil 299, 153–162.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.H., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., can Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.N., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065–1071.

Cowling, R.M., Lombard, A.T., 2002. Heterogeneity, speciation/extinction history and climate, explaining regional plant diversity patterns in the Cape Floristic Region. Diversity and Distributions 8, 163–179.

Cowling, R.M., Richardson, D.M., Muster, P.J., 1997. Fynbos. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), The Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 99–130.

Enríquéz, S., Duarte, C.M., Sand-Jensen, K., 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94, 457–471.

Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M.-M., Roy, J., Bonal, D., 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. New Phytologist 179, 165–175.

Joffre, R., Ågren, G.I., 2001. From plant to soil: litter production and decomposition. In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), Terrestrial Global Productivity. Academic Press, pp. 83–99.

Jonsson, M., Wardle, D.A., 2008. Context-dependency of litter-mixing effects on decomposition and nutrient release across a long-term chronosequence. Oikos 117, 1674–1682.

Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., Garnier, E., 2009. Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. Annals of Botany 104, 1151–1161.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556.

Linder, H.P., 2003. The radiation of the Cape flora, southern Africa. Biological Reviews 78, 597–638.

Manning, J., 2007. Field Guide to Fynbos. Struik, Cape Town, South Africa.

Mitchell, D.T., Coley, P.G.F., 1987. Litter production and decomposition from shrubs of *Protea repens* growing in sand plain lowland and mountain fynbos, south-western Cape. South African Journal of Botany 53, 25–31.

Mitchell, D.T., Coley, P.G.F., Webb, S., Allsopp, N., 1986. Litter fall and decomposition processes in the coastal fynbos vegetation, south-western Cape, South Africa. Journal of Ecology 74, 977–993.

Mucina, L., Rutherford, M.C. (Eds.), 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African national Biodiversity Institute, Pretoria.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Osler, G.H.R., Sommerkorn, M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88, 1611–1621.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C., Fasth, B., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315, 361–364.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L., Rutherford, M.C., 2006. Fynbos biome. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, pp. 52–219.

Richards, M.B., Stock, W.D., Cowling, R.M., 1997. Soil nutrient dynamics and community boundaries in the Fynbos vegetation of South Africa. Plant Ecology 130, 143–153.

Richardson, D.M., van Wilgen, B.W., 1992. Ecosystem, community and species response to fire in mountain fynbos: conclusions from the Swartboskloof experiment. In: Van Wilgen, B.W., Richardson,, D.M., Kruger, F.J., Hensbergen, H.J. (Eds.), Fire in South African Fynbos. Springer, pp. 273–284.

Simons, L., Allsopp, N., 2007. Rehabilitation of rangelands in Paulshoek, Namaqualand: understanding vegetation change using biophysical manipulations. Journal of Arid Environments 70, 755–766.

Sokal, R.R., Rohlf, F.J., 1991. Biometry, second ed. Freeman, New York.

Stock, W.D., Allsopp, N., 1992. Functional perspective of ecosystems. In: Cowling, R.M. (Ed.), The Ecology of Fynbos: Nutrients, Fire and Diversity. Oxford University Press, Cape Town, pp. 241–259.

Stock, W.D., Lewis, O.A.M., 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. Journal of Ecology 74, 317–328.

Todd, S.W., Hoffmann, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecology 142, 169–178.

Van der Lugt, J.J., Schultz, R.A., Fourie, N., Hon, L.J., Jordaan, P., Labuschagne, L., 1992. *Galenia africana* L. poisoning in sheep and goats: hepatic and cardiac changes. Journal of Veterinary Research 59, 323–333.

van Wilgen, B.W., le Maitre, D.C., 1981. Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. South African Forestry Journal 119, 24–28.

van Wilgen, B.W., 2009. The evolution of fire and invasive alien plant management practices in fynbos. South African Journal of Science 105, 335–342.

Vries, F.A., El Bitar, H., Green, L.R., Klaasen, J.A., Mabulesa, W.T., Bodo, B., Johnson, Q., 2005. An antifungal active extract from the aerial parts of *Galenia africana*. In: Midiwo, J.O., Yenesew, A., Derese, S. (Eds.), 11th NAPRECA Symposium Book of Proceedings, Antananarivo, Madagascar, 2005. Napreca, Nairobi, Kenya, pp. 123–131. www.napreca.net.

Wardle, D.A., Bardgett, R.A., Walker, L.R., Bonner, K.I., 2009. Among and within plant species variation in plant litter decomposition in contrasting long-term chronosequences. Functional Ecology 23, 442–453.

Witkowski, E.T.F., 1989. Effects of nutrient additions on litter production and nutrient return in a nutrient-poor Cape fynbos ecosystem. Plant and Soil 117, 227–235.

Witkowski, E.T.F., 1991. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. Journal of Applied Ecology 28, 1–15.