



# The response of springtails to fire in the fynbos of the Western Cape, South Africa



Charlene Janion-Scheepers<sup>a,e,\*</sup>, Jan Bengtsson<sup>b</sup>, Hans Petter Leinaas<sup>c</sup>, Louis Deharveng<sup>d</sup>, Steven L. Chown<sup>a,e</sup>

<sup>a</sup> Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag XI, Matieland, 7602, South Africa

<sup>b</sup> Swedish University of Agricultural Sciences, Department of Ecology, Box 7044, SE-750 07, Uppsala, Sweden

<sup>c</sup> Department of Biosciences, University of Oslo, Box 1066, N-0316, Oslo, Norway

<sup>d</sup> Institut de Systématique, Évolution, Biodiversité ISYEB – UMR 7205 – CNRS, MNHN, UPMC, EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, 45 Rue Buffon, F-75005, Paris, France

<sup>e</sup> School of Biological Sciences, Monash University, Victoria 3800, Australia

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## ABSTRACT

Although fire is a natural form of disturbance in many ecosystems, the frequency of fires is increasing due to human activities. Hence, understanding the impacts of fire on biodiversity and ecosystem functioning has become increasingly important. In this study we investigated the effects of a large-scale fire on an important soil-dwelling group, springtails (Collembola), one year before and for three consecutive years after a fire in the fire-prone fynbos ecosystem in South Africa. In particular, we investigate the resistance of the springtail assemblages (i.e. their ability to remain relatively unchanged in the face of a disturbance), and their resilience (i.e. ability to return to a pre-disturbance state). To do this we sampled two sites with contrasting vegetation (*Erica* and *Protea*) and used three different standardized litter types in litterbag traps. A total of 35 springtail species from 31 genera and 14 families was found. The springtail assemblages in this fynbos system showed slightly more resistance to fire than resilience after the fire event, though substantial variation was found among vegetation types. Mean species richness and abundance per litterbag varied among the *Protea* and *Erica* sites, with resistant species being dominant in the *Erica* site, while species that showed an increase after the fire were dominant in the *Protea* site. Differences were also found between life forms: atmobiotic (free-living in vegetation) and epiedaphic (surface dwelling) species showed a significant decline in mean species richness directly after the fire in the *Erica* site. Euedaphic (soil-dwelling) species richness remained unchanged post-fire in the *Erica* site, while actually slightly increasing after the fire in the *Protea* site. Although the fynbos springtail assemblages had not fully recovered to pre-fire abundance after three years, many species appear to be resistant to or recover rapidly after fires, at least as ascertained over the relatively short (four years) duration of the study. It is likely that this response is influenced by the presence of suitable refugia within sites and by species-specific traits. Given changing fire regimes and the increasing frequency of fires due to human disturbances, the system will likely become more dominated by resistant springtail species preferring nutrient rich circumstances and easily decomposed litters.

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## 1. Introduction

In many ecosystems, fire is a major natural form of disturbance. Although fire has been used by humans to alter landscapes for a long time (Bond et al., 2005), in many areas fire regimes have been

altered substantially over the last several decades (Goldammer and Price, 1998; Syphard et al., 2009). Often these changes have been associated with specific conservation management goals. Indeed, fire is widely used as a tool for biodiversity management in protected areas (Pastor et al., 2011; Kelly et al., 2012). Evidence is growing, however, that fire regimes are also shifting as a consequence of changing climates and growing human populations (Stocks et al., 1998; Running, 2006; Syphard et al., 2009;). The fire-prone fynbos vegetation of the Western Cape of South Africa provides a clear example of this trend. Fires usually occur at

\* Corresponding author at: School of Biological Sciences, Monash University, Victoria 3800, Australia.

E-mail address: [charlene.janionscheepers@monash.edu](mailto:charlene.janionscheepers@monash.edu) (C. Janion-Scheepers).

intervals of 10–15 years (van Wilgen, 2009; van Wilgen et al., 2010; Kraaij et al., 2011; van Wilgen, 2013). However, now it appears that, whether or not management attempts are made to alter the fire cycle, fire frequency is increasing substantially (van Wilgen, 2009; van Wilgen et al., 2011). This is resulting in, for example, repeated short intervals between fires ( $\approx$ five years) affecting vegetation dynamics in the fynbos (van Wilgen, 2013).

Despite these changes, and the significance of fire worldwide as a major influence on diversity (Pastro et al., 2011; Fontaine and Kennedy, 2012) and soil properties (Certini, 2005), current knowledge of the effects of fire on soil invertebrates is poor. Understanding how biodiversity is responding and will continue to respond to changing disturbance regimes is a key prerequisite for evidence-based conservation (Hobbs and Heunneke, 1992). Such conservation is essential if diversity is to be retained in the face of increases in the extent and scope of environmental change (MEA, 2005; Butchart et al., 2010). Developing knowledge across a broad range of taxa is especially important for reducing uncertainty about how responses might vary among different functional groups, both for their conservation and for understanding how these responses will affect ecosystem functioning (Decaëns et al., 2006; Bardgett and van der Putten, 2014). In the case of fire, much work has been done on the response of vegetation and groups such as birds and mammals (Dean, 1987; Bond, 1997; Root et al., 2003; Bond et al., 2005; Pastro et al., 2011). For some invertebrate groups similar understanding is being developed across a wide range of ecosystems globally. Ant assemblages provide a notable example of this (Parr et al., 2004; Parr and Andersen, 2008; Lach et al., 2009; Vasconcelos et al., 2009; Andersen and Müller, 2000; Andersen et al., 2014). By contrast, for many other invertebrate groups, such as soil-dwelling ones, investigations are more limited. This makes generalizations of post-fire responses of soil-dwelling fauna problematic, despite the functional significance of these groups (Parr and Chown, 2003; Zaitsev et al., 2016).

Soil organisms play a major role in global ecosystem functioning (Bardgett and van der Putten, 2014). An important group among them are springtails (Collembola), which contribute in a variety of ways to system functioning, such as facilitating litter decomposition and the formation of soil microstructure (Hopkin, 1997; Rusek, 1998). Although their role in soil ecosystems is widely appreciated, their importance in soil ecosystem functioning is difficult to underestimate, while not much is known about springtail assemblage response to fire. Current consensus, that springtail abundance initially decreases significantly after fire and gradually increases again, is derived mostly from investigations in boreal and temperate forests of Europe and North America (Moretti et al., 2006; Malmström et al., 2009; Malmström, 2010; Huebner et al., 2012; Malmström, 2012). The speed of recovery has been shown to depend on fire intensity (Malmström, 2010), and some species seem to be resilient (Renschin et al., 2004). How springtail assemblages elsewhere respond to fire is, however, not completely understood (but see Driessen and Greenslade, 2004; Greenslade and Smith, 2010).

Here we examine the effects of a large-scale fire on the springtail fauna of a fynbos ecosystem in the Western Cape of South Africa, using a study including information from before the fire and then for a period of three years after it. Earlier studies on the response of invertebrates to fire in this system have focused on insects (Donnelly and Giliomee, 1985; de Kock et al., 1992; Pryke and Samways, 2012). The responses of other arthropod groups remain largely unknown, or at best understood at the scale of response of entire higher taxa such as families (Pryke and Samways, 2012). By contrast, little is known about significant soil-dwelling taxa, such as springtails, which are known to be highly diverse and ecologically significant in this region (Janion et al., 2011a; Janion-Scheepers et al., 2015; Leinaas et al., 2015). In

particular, we investigate the resistance of the springtail assemblages (i.e. their ability to remain relatively unchanged in the face of a disturbance), and their resilience (or ability to return to a pre-disturbance state), with resolution to the species level. Resilience has been used in several different ways in ecology (Grimm and Wissel, 1997). Here we follow the use of Pimm (1991), defining resilience as the rate at which a population returns to a previous value, and resistance as the amount a population or assemblage changes in response to an environmental change. DeAngelis (1980) applied a similar definition of resilience to ecosystems. These uses differ from the way in which Holling (1973) and Scheffer et al. (2015) define resilience – the extent to which a chance event (such as a fire) might trigger a dramatic change in the system. Nonetheless, it is clear what the similarities and differences are in these usages, enabling them to be compared readily.

The major vegetation types of the fynbos produce litter, which differ in amount, texture and nutrient quality (Bengtsson et al., 2012). Since this might possibly affect both immediate and secondary effects of fire on the animals, we studied resistance and resilience of springtails at two sites with contrasting vegetation and used three different standardized litter types in litterbag traps (Leinaas et al., 2015). In particular we tested the hypothesis, in keeping with work elsewhere on soil invertebrates in fire-prone systems (e.g. Parr et al., 2004), that springtail assemblages in fynbos include populations of species that are resistant and those that are resilient to fire, such that assemblages overall appear relatively resilient to fire, returning to the pre-fire state within the typical period between fires. To do so we addressed three primary questions: 1. To what extent does abundance change in each of the species constituting the assemblages in different vegetation types in response to the fire and following it? 2. How common is resistance compared with resilience, acknowledging our relatively short-term, i.e. 4-year, sampling period? 3. What form of change does assemblage diversity take in the different vegetation types in response to the disturbance and following it?

## 2. Methods

### 2.1. Study sites and experimental technique

The study was carried out from 2008 to 2011, with sampling during the winter months (mid-March to mid-September) in Jonkershoek Nature Reserve, South Africa (S33.989112°, E 18.957535°), which is approximately 9 km from Stellenbosch and encompasses 14 527 ha (van Wilgen and 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). Mean temperature of the reserve is 16.2 °C (lowest minimum 0.2 °C and highest maximum 39 °C) with a total annual precipitation of 1523 mm (Versfeld et al., 1992). The vegetation consists of mainly mountain fynbos (Rebelo et al., 2006) surrounded by the Jonkershoek Mountains (> 1000 m), has over 1100 plant species and a high diversity of animals, birds and reptiles (Versfeld et al., 1992).

To assess the diversity and distribution of springtails, the litterbag method was used for sampling (Bocock and Gilbert, 1957). Litterbags have been used widely to study soil fauna and decomposition rates (Crossley and Hoglund, 1962; Wall et al., 2008). Although other standard methods such as Tullgren-Berlese funnels and vegetation beating are often used to collect springtails, this study also investigated the effect of different litter types on springtail abundance and species richness (see Bengtsson et al., 2012). More extensive sampling has been done in the same region using a combination of collection techniques (Janion-Scheepers

et al., 2015). In the present study, the litterbag traps consisted of individually numbered cylindrical plastic containers with a height of 4 cm and a diameter of 7.5 cm, a removable lid with steel mesh size (1.6 mm) to allow animals to enter the litterbags, and a lower steel mesh size of 0.5 mm (Supplementary material Fig. S1A, B; also see Leinaas et al., 2015). It has been shown that springtails differ in abundance and richness between different litter types (Wall et al., 2008; Fujii and Takeda, 2012). Three different litter types were used to measure springtail diversity (see Bengtsson et al., 2011, 2012), chosen to represent the three major plant types characteristic of the fynbos (see Rebelo et al., 2006). The first litter type consisted of a 1.3:1 ratio of *Erica multumbellifera* (Ericaceae), and a hybrid *Protea exima* x *Protea susannae* (Proteaceae), var. “silva” and “cardinal” mix, (Bengtsson et al., 2012). The *Erica* litter was collected at Heuningbos, Kleinmond (S34.330600°, E19.060950°), the hybrid *Protea* litter from Flower Valley Farm, Stanford (S34.548923°, E19.470345°). The second litter type consisted of *Restio multiflorus* (Restionaceae), collected at White Water Lodge, Stanford (S34.4048996°, E19.53969955°). A third litter type was also included, namely *Galenia africana* (Aizoaceae), a common shrub in the Western Cape. It is an indicator of disturbance such as overgrazing and has a high decomposition rate (Allsopp, 1999; Bengtsson et al., 2011; 2012). This species was collected from an overgrazed rangeland west of the Paarl Mountain (S33.727436°, E18.893114°), where it is the dominant shrub in the vegetation. *Galenia africana* was used as a standard litter to be compared among sites, and to include a nutrient rich litter as has been done previously (Bengtsson et al., 2011, 2012; Leinaas et al., 2015).

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 was taken to the laboratory, dried at 40° C for at least 24 h 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 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 masses of litter per bag 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. For further details, see Bengtsson et al. (2012).

Two study sites were selected, approximately 200 m apart, with different dominant vegetation types. In this study we were able to sample two of the three characteristic vegetation types in the Fynbos, namely proteoid and ericoid (the third type, restioid, could not be sampled after the fire due to flooding). One proteoid site was selected, dominated by *Protea nitida*, while the other site was ericoid, dominated by *Erica hirta* (see Supplementary material Figs. S2A, B). Three litterbags each containing a different litter type (*Protea-Erica* mixture, *Restio* 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 the austral spring. Litterbags were deployed in an L-shape transect (estimated sample unit coverage of 2500 m<sup>2</sup>) to cover a wide 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. S3). This design was chosen as part of a geographically large-scale study on springtail diversity in the fynbos (Janion, 2013). Each tree or shrub underneath which litterbags were deployed was approximately 10 m apart. The litterbags were deployed under the trees or shrubs within 3–4 cm from each other, less than 40 cm from the plant 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. 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, after the first winter sampling event, 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. S2). The fire in this study was a single wildfire, thus spatial replication, for control and impacted sites, was not possible. Indeed, studies of this kind obtaining data before and after a wildfire data are rare, whilst controls and replications are almost impossible (Parr and Chown, 2003; Zaitsev et al., 2016). 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 and McDonald, 1992). After the fire in 2009, litterbags were again 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. S4, S5). We consider our time of series of samples representative due to the recent change of the fire frequency from 10 to 15 years to 5 years (Forsyth and van Wilgen, 2010).

Following collection, litterbags 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 transported to the laboratory within two hours of collection. Here they were extracted using a modified high-gradient extractor (custom-built by Central Mechanical Services, Stellenbosch Engineering, Stellenbosch University, following designs used by Leinaas et al. (2015)). 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 four days. The litterbags were inverted in the high gradient extractor with heating from above (see Macfadyen, 1953; Leinaas, 1978) and cooling from below by means of a temperature controlled water bath (Grant R2, Cambridge, UK). The high gradient extractor temperature was set at 25° C when the litterbags were inserted, then gradually increased to 50° C over a period of four days and was monitored throughout. The extraction was done into 100% propylene glycol, thereafter the animals were transferred to 99.9% ethanol for identification. The dry litter samples were removed for chemical analyses (for details see Bengtsson et al., 2012).

Morphospecies and, if possible, species (all referred to hereafter as species) were identified using taxonomically significant morphological characters and European keys available to determine the family and genus (Fjellberg, 1998, 2007; Bretfield, 1999; Potapov, 2001; Hopkin, 2007). In addition, taxonomic specialists on groups with which the systematic experts among the authors (LD, CJS) were not fully familiar, were consulted on a regular basis as part of an existing knowledge transfer project (see Janion et al., 2011a).

## 2.2. Data analyses

As the possibility exists of animals breeding in the litterbag, which may result in an artificially high abundance, we chose not to include data from samples containing over 2000 individuals to remove any bias caused by breeding in the litterbag. Thus, data from eight samples out of the 260 were removed prior to analyses, as each of these samples contained over 2000 individuals of *Cryptopygus* sp. (seven samples) or *Triacanthella* sp. (one sample), which mostly contained juveniles. This occurred in two litterbags in the *Protea* site (2010: one *Erica-Protea* mix, 2011: one *Galenia*), and six in the *Erica* site (2010: two *Galenia* and one *Restio*, 2011: one *Galenia*, one *Restio* and one *Erica-Protea* mix).

Sampled-based rarefaction curves were used to examine the degree of sampling efficiency and to determine the predicted number of species in each site in each year using EstimateS V8.2.0 (Colwell, 2009). The Chao1 and Jackknife 2 estimators were also calculated. Jackknife 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).

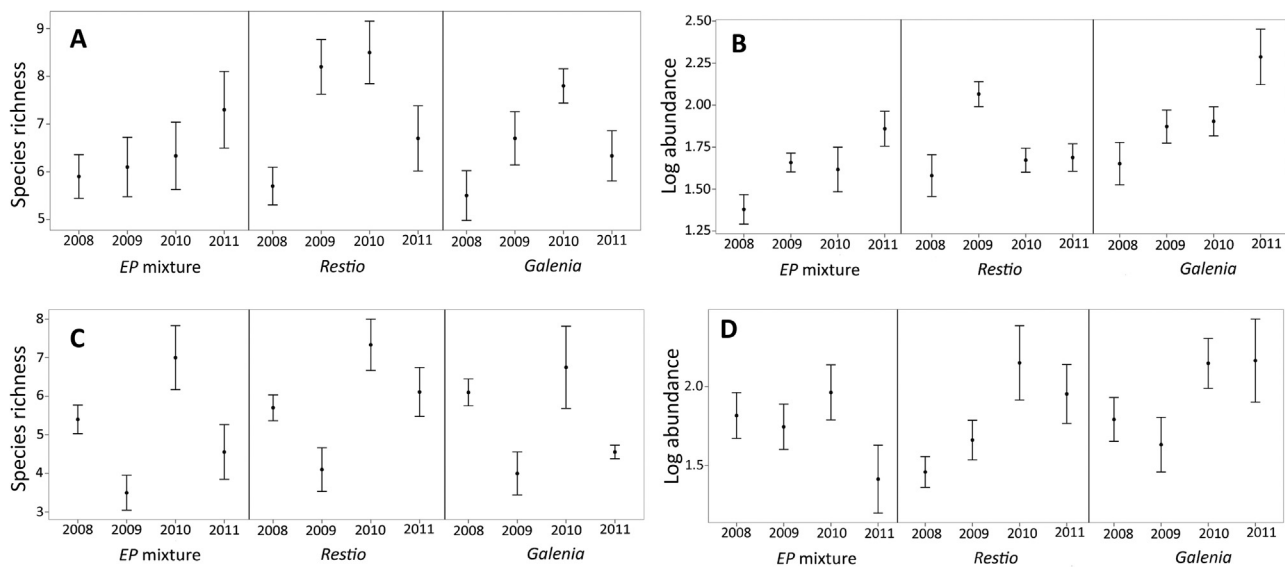
As the two sites have different habitat types, and to determine how assemblages differ between the two sites, we analysed each site separately. To investigate how species richness and abundance changed post-fire, we tested the effect of year (i.e. fire) and litter type on the species richness and abundance of springtails. Abundance data were log transformed prior to analyses. For each site, we used generalized linear models (GLM) to analyse the effect of the fire (year) and litter type on the species richness and abundance (R Core Team, 2015). We also used a linear mixed effect model with litter as a random factor and year as a fixed factor to compare models.

Springtails are divided into different life forms based on their distribution in the soil layer (Hopkin, 1997). It has also been shown that different life forms respond differently to disturbances such as fire (Malmström, 2012). Therefore, the effect of fire on the species richness and abundance of the different life forms was investigated by dividing the species into three major life forms after Gisin (1943, modified), namely euedaphic (soil dwelling), epiedaphic (surface dwelling, that corresponds to the “mesophil hemiedaphon” of Gisin, 1943) and atmobiotic (free living in the vegetation). To investigate how species richness and abundance changes post-fire in each life form group within each site, we tested the effect of year (i.e. fire) and litter type using generalized linear models. All analyses (also see below) were undertaken in R V3.1.1 (R Core Team, 2015).

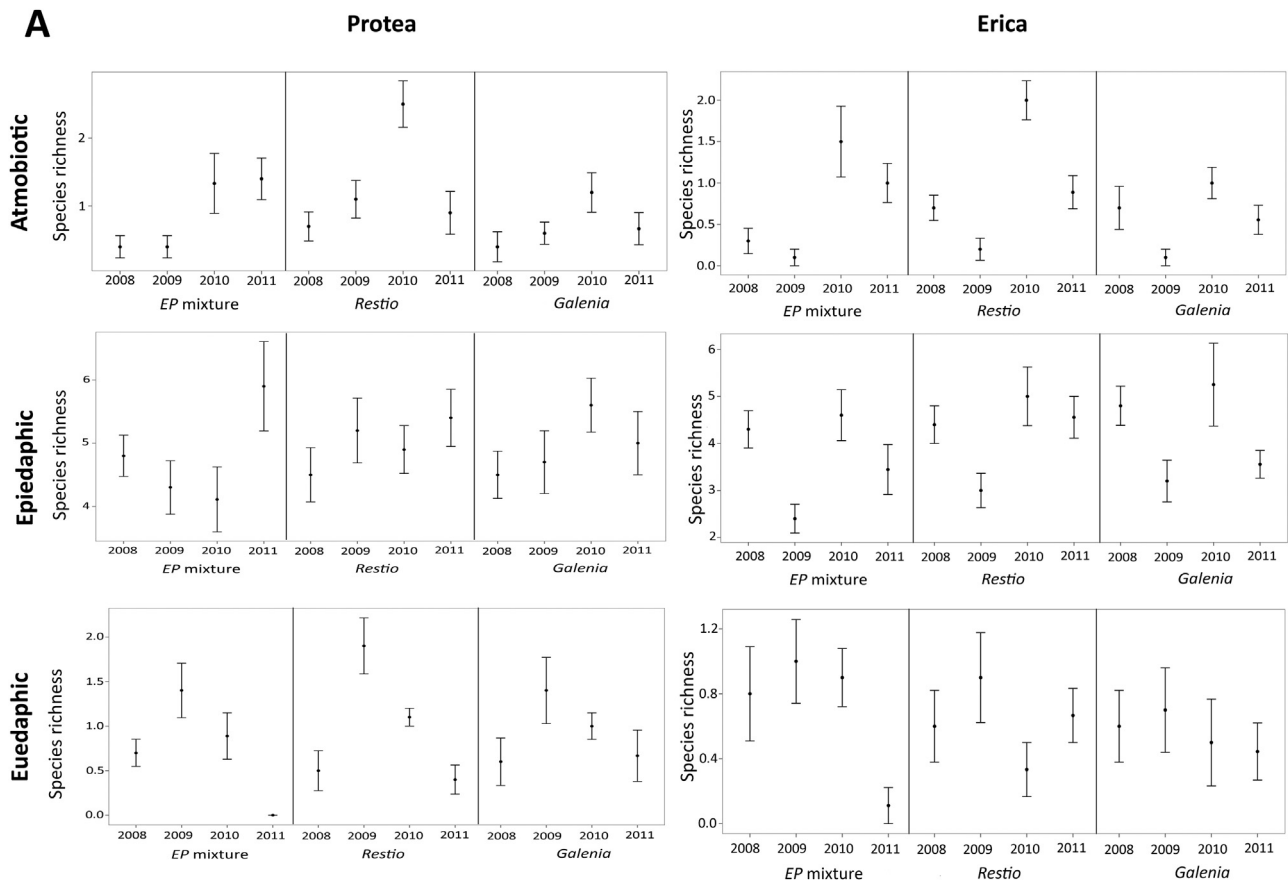
To understand the extent of resistance and resilience (in terms of recovery after the disturbance; see Pimm 1991 for definitions) of the different species, and overall assemblage response to fire we examined the variability in the abundance of species. Because abundance may vary for many reasons (Gaston and McArdle, 1994), the responses of the species among years and sites were assessed using two different approaches, in particular to account for

variation that may simply be inherent to any particular system. First, species abundances were compared using a categorical approach based on a log scale, which means that variability in abundance through time can be compared among populations which differ substantially in initial population size (Gaston and McArdle 1994). For each site and year, species were grouped into the following categories: (a) singletons ( $\leq 4$  individuals), (b) static species (i.e. resistant species that do not change on a logarithmic scale between years), (c) boom species (species that increase by at least two on a logarithmic scale and then decline), (d) resilient species (species that change by at least one on a logarithmic scale and then revert), (e) species that show an increase by at least one on a logarithmic scale (increase) and lastly (f) species declining by at least one on a logarithmic scale (decline). Importantly, the extent of variability among species was not being compared directly to understand whether one species was significantly more variable than another. Such analyses require understanding of the relationships among means and variances (Gaston and McArdle 1994), and a longer time series from the pre-fire period, but we sought here only to categorize the variation in abundance within species. The second approach was more simple, and compared species replacement among years and sites, using estimates of beta diversity.

To investigate the effect of fire on the assemblage over time we calculated the species turnover (i.e. change in species identity) among years in each site, before the fire, immediately after it, and in the subsequent years. To do this we followed the methods recommended by Baselga (2010, 2012). Here, dissimilarity due to nestedness ( $\beta_{sne}$ ) is distinguished from dissimilarity due to turnover or species replacement (Simpson dissimilarity,  $\beta_{sim}$ ) (Baselga, 2010). The *betapart* package in R V3.1.1 was used to calculate these and to plot a hierarchical cluster dendrogram (Baselga and Orme, 2012; Baselga et al., 2013). Studies on ants in savanna systems have shown little change in species composition after fire (Parr et al., 2004; Andersen et al., 2014). However, as springtails can be severely affected by fire (Malmström et al., 2009; Huebner et al., 2012; Malmström, 2012), we expected that turnover would be highest among sampling events before and after the fire, after which assemblages would become less dissimilar as they recovered over time.



**Fig. 1.** Collembola mean  $\pm$  S.E. (A) species richness and (B) log abundance per year in the *Protea* site, Collembola mean  $\pm$  S.E. (C) species richness and (D) log abundance per year in the *Erica* site. Litter type EP = *Erica-Protea* mixture. The fire occurred in 2009.



**Fig. 2.** The variation in springtail (A) Species richness and (B) abundance for each site, litter, and year for the three different life form groups. Litter type EP = *Erica-Protea* mixture. The fire occurred in 2009.

The Indicator Value Method (Dufrene and Legendre, 1997) was used further to assess the extent to which species turned over among years. Specifically, to investigate the resistance of the assemblage, the most characteristic species per year and site was determined. This method calculates the indicator value based on the frequency and abundance of species, and was calculated using the *labdsv* package in R Version 3.1.1. If the assemblage is resistant to fire, the indicator values should remain consistent before and after the fire and over the years. A high IndVal indicates a species is characteristic of the habitat or site. This method is not only useful to indicate if a species is representative of the site, but also includes a measure of habitat fidelity (frequency of occurrence) (McGeoch et al., 2002). Species with IndVal values higher than 70% are considered characteristic of a site (Dufrene and Legendre, 1997).

To determine how the fire affected overall variation in the springtail assemblage composition among years per site, multivariate analyses were undertaken in Primer V.6.0 (Clarke and Warwick, 2001). Data were square root transformed to reduce the weight of the common species (Clarke and 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 significant differences among springtail assemblages between years before and after the fire. A nested ANOSIM was chosen, with litter nested within years. Global R values obtained from ANOSIM were used to determine the degree of similarity between years. 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 nearly indistinguishable. A non-metric multi-dimensional scaling (nMDS) ordination was used to visualize the

differences among years. This analysis was repeated using presence-absence data only, further to distinguish the effects of the most abundant species. Temperature and rainfall data over the study period is shown in Supplementary material Fig. S6.

### 3. Results

#### 3.1. Abundance and species richness

A total of 31,910 springtails, comprising 35 species in 31 genera and 14 families was found in this study (Fig. 1, Supplementary Table S1). Total number of individuals and species for the years was: 2008: 3871 (25 species); 2009: 4905 (26 species); 2010: 11,999 (26 species); 2011: 11,135 (27 species). The sample-based rarefaction curves reached an asymptote in most cases, indicating that species were sampled approximately to near completion (Supplementary material Figs. S7A–D). Mean species richness per litterbag varied significantly from a high value of  $8.5 \pm 0.65$  in the *Protea* site to a low value of  $3.5 \pm 0.45$  (mean  $\pm$  standard error) in the *Erica* site (Fig. 1). Mean abundance per litterbag also showed much variation from  $471.89 \pm 201.62$  to  $28.9 \pm 6.28$  in *Erica* and *Protea* sites, respectively (Fig. 1). However, high abundance during the second and third year after the fire were mainly driven by a few species, such as *Triacanthella* sp. in the *Protea* site and *Cryptopygus* sp. in the *Erica* site (Supplementary material Table S2).

At the *Erica* site, the fire influenced species richness, which decreased significantly in the year of the fire (Fig. 1C, Supplementary Table S1, S3). Abundance did not decrease significantly, but increased two and three years after the fire in the *Restio* litter (Supplementary Table S3). In contrast, in the *Protea* site species

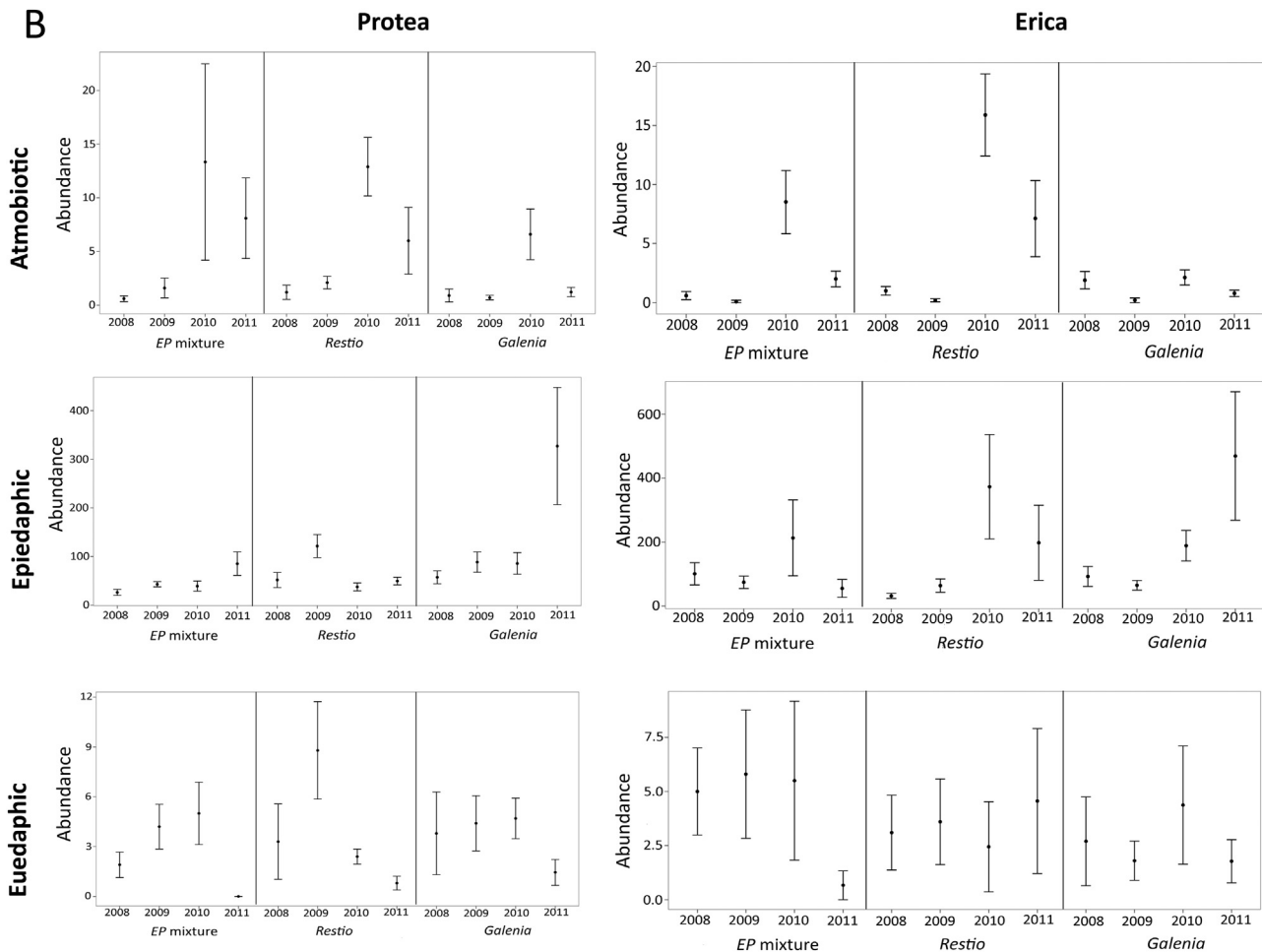


Fig. 2. (Continued)

richness did not decrease in the year of the fire, but actually increased in the *Restio* litter (Fig. 1A, Supplementary Table S1, S3). Also, springtail abundance did not decline due to fire, but increased in all litter types.

### 3.1.1. Life forms: abundance and species richness

Euedaphic species showed either no response or an increase in species richness and abundance in all litter types after the fire in both sites (Fig. 2A, B, Supplementary Table S4.1, S4.2). Overall there was no significant increase in abundance in post-fire years, but there were a few exceptions such as the very high abundance in the epiedaphic species in the *Galenia* litter two years after the fire in both sites (Fig. 2B). In the *Erica* site species richness declined after the fire in the atmobiotic and epiedaphic groups and subsequently increased again, while the euedaphic species showed no significant effect with any of the litter types (Fig. 2A, B, Supplementary Table S4.2). The atmobiotic and epiedaphic species showed an increase in abundance one year and two years after the fire. The abundance of the euedaphic species did not change significantly post-fire.

The most common species (*Triacanthella* sp., *Brachystomella* sp., *Isotomurus* sp., *Mesaphorura* sp., *Lepidocyrtus* sp., *Cryptopygus* sp. 1, *Seira* sp. 1 and *Parisotoma* sp.) were present in both *Erica* and *Protea* sites before and after the fire. Some species were only present before the fire (e.g. *Hypogastura* sp.), while others were only present after the fire (e.g. *Setanodosa* sp., Supplementary material,

Fig. S8). This was also illustrated by the IndVal values (Supplementary Table S5). For example, in the *Protea* site, species such as *Lepidocyrtus* sp. and *Parisotoma* sp. were characteristic throughout the years, while others had high values before, but not after the fire (e.g. *Sminthurinus* sp. 1).

### 3.1.2. Assemblage composition

By the categorical method adopted here, 29% of the species were considered resistant (as defined by Pimm, 1991), 21% were resilient, 21% were boom species, and the remainder showed another response. When calculating the variation in species abundance over time using the five logarithmic categorical classes (Table 1), the *Protea* site had more resilient species than the *Erica* site (seven species vs. two species), while the *Erica* site had a greater number of resistant species (nine vs. three species, Table 1). Both sites had two 'boom' species each, which included *Austrogastura* sp. and *Isotoma* sp. in the *Protea* site and *Austrogastura* sp. and *Proisotoma* sp. in the *Erica* site (Table 1). Overall, most species found in the *Protea* site fell into the 'increase' category (32%), while the higher percentage (38%) of species were in the resistant category in the *Erica* site.

The ANOSIM results for the *Protea* site indicated that the springtail assemblage not only differed significantly in abundance between years when using square root transformed abundance data (Global R=0.843,  $p < 0.05$ , Fig. 3A), but also when using presence-absence data (Global R=0.64,  $p < 0.05$ , Fig. 3B). Similar

**Table 1**

The percentage of Collembola species per category (see below) following the fire event with the number of species in parentheses (excluding singletons). Categories as follows: species that show an increase, species that show a decline, resilient species (species that change by one log class and then revert), boom species (species that increase by two log classes and then decline), static or resistant species (do not change log class between years) and singletons ( $\leq 4$  individuals).

	Protea and Erica sites combined	Protea site	Erica site
Increase	18% (5)	32% (8)	25% (6)
Decline	11% (3)	20% (5)	21% (5)
Resilient	21% (6)	28% (7)	8% (2)
Boom	21% (6)	8% (2)	8% (2)
Resistant	29% (8)	12% (3)	38% (9)
Singletons	7	9	7
Total no. species	35	34	31

results were found for the *Erica* site (square root transformed data Global  $R=0.775$ ,  $p < 0.05$ , Fig. 3C; presence-absence data Global  $R=0.583$ ,  $p < 0.05$ , Fig. 3D).

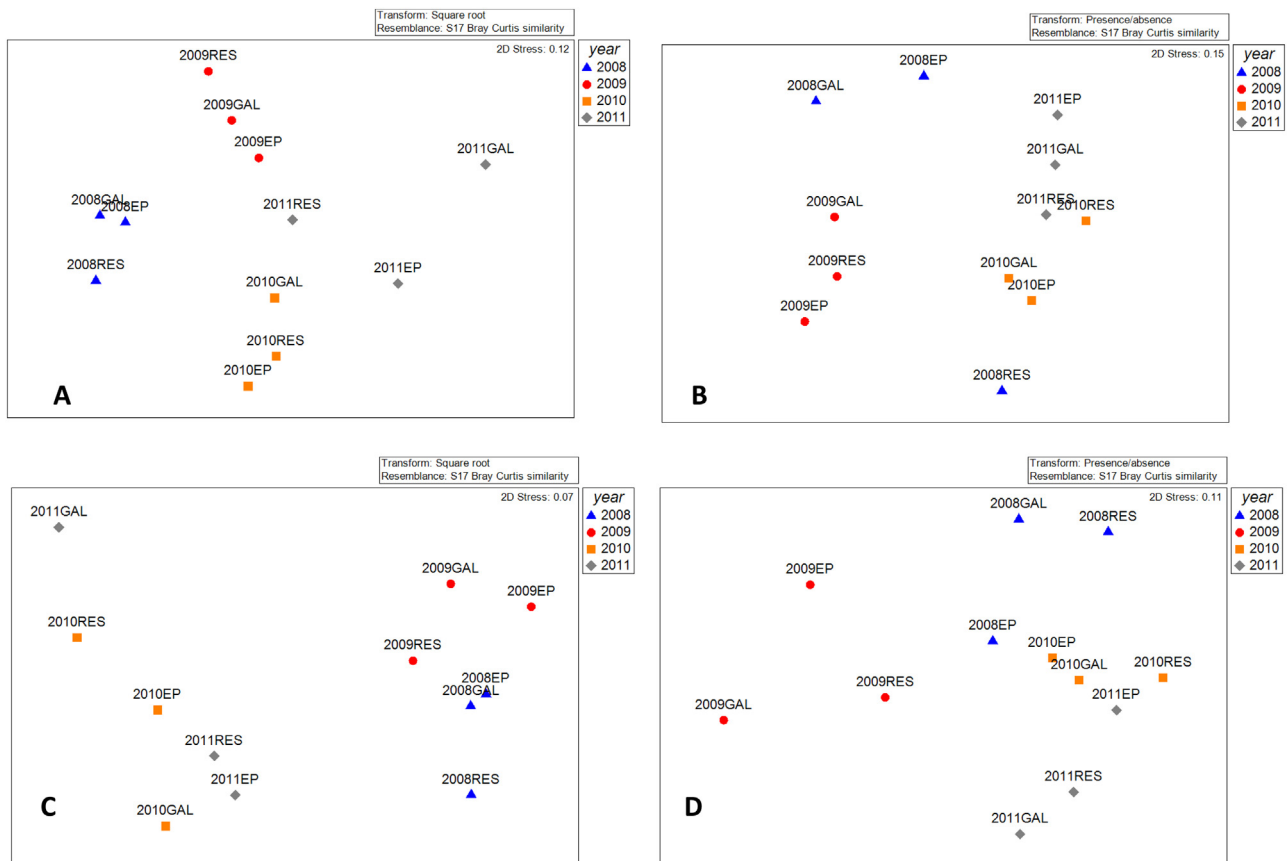
In the *Protea* site, species composition was more similar two and three years after the fire than before or one year after the fire, thus the dissimilarity due to turnover ( $B_{sim}$ ) was high between these years (Fig. 4). Dissimilarity due to nestedness ( $B_{sne}$ ) was greatest one or three years after the fire and before or two years after the fire (Fig. 4). In the *Erica* site, species composition was more similar before or two years after the fire than one year or three years after the fire (Fig. 4). Dissimilarity due to nestedness

( $B_{sne}$ ) was greatest before or one year after the fire and two or three years after the fire (Fig. 4).

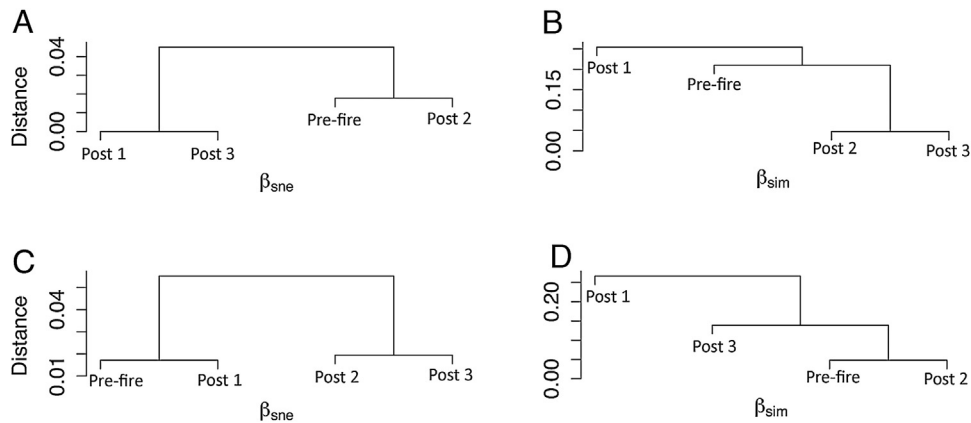
#### 4. Discussion

In this study we had the unique opportunity to obtain data on springtail diversity before and for three years after an unplanned wildfire. Several species were continuously present throughout the study sites, indicating they are least vulnerable to fire. Although these resistant species showed little change owing to the fire, overall abundance of the total assemblages responded strongly with dramatic declines directly after the fire and then recovery. In consequence, the assemblages overall showed resilience to the effects of a single, large wildfire. The dissimilarity due to turnover ( $B_{sim}$ ) among years was especially notable as an indicator of this among-year change. Nonetheless, the changes varied among the *Protea* and *Erica* sites, with resistant species being dominant in the *Erica* site, while species that showed an increase were dominant in the *Protea* site. Overall, it appeared that abundance returned within three years here to initial values, but with considerable variation among species. Although the study had limited spatial replication, having data before and after the fire adds confidence to our conclusions about the responses of the springtail assemblages, at least for this relatively short-term investigation.

In boreal forests, post-fire species richness recovery for springtails was found to be relatively rapid (one year) in terms of total abundance, depending on the fire severity (depth of burn), which has pronounced impact on the litter layer, while fire



**Fig. 3.** Non-metric multidimensional scaling (nMDS) plots of springtail assemblages in different litter types in the *Protea* site pre-fire (2008) and one, two and three years after the fire (2009, 2010 and 2011) using square root transformed abundance data (A) and presence-absence data (B), and in the *Erica* site pre-fire (2008) and one, two and three years after the fire (2009, 2010 and 2011) using square root transformed abundance data (C) and presence-absence data (D). Litter type EP = *Erica-Protea* mixture, RES = *Restio*, GAL = *Galenia*.



**Fig. 4.** Dendrograms for beta diversity of dissimilarity of each site between years due to (A) nestedness ( $\beta_{sne}$ ) and (B) species replacement ( $\beta_{sim}$ ) in the Protea site; (C) nestedness ( $\beta_{sne}$ ) and (D) species replacement ( $\beta_{sim}$ ) in the Erica site. Abbreviations used: Pre-fire = before the fire (2008), Post 1 = one year after the fire (2009), Post 2 = two years after the fire (2010), and Post 3 = three years after the fire (2011). An increase in branch length indicates an increase in dissimilarity.

intensity (heat release) has a more pronounced impact on animal survival (Malmström et al., 2008). For severe fires in boreal forests, full recovery in assemblages was not found for springtails even after a 10-year period (Malmström, 2012). Thus, the springtail assemblages investigated in this fynbos system appear to recover more rapidly than those of boreal forests that have experienced severe fires. A likely explanation is the difference in historical fire frequency, which is in the order of 10–20 years in fynbos (van Wilgen et al., 2010), but 70–100 years in boreal forests (Kelly et al., 2013), which is likely to make most fynbos species adapted to fires at these intervals. In addition, several environmental factors such as temperature, rainfall and soil chemistry may play an important role in post-fire recovery, which in turn may affect springtail generation times.

The percentage of species found to be resistant to the fire in this study (29%), is fairly similar to that found for springtail assemblages in habitats elsewhere, such as boreal forests in Sweden (Malmström et al., 2009; Gongalsky et al., 2012). This may be due in part to the availability of refugia for post-fire recovery, while these two different systems contain similar springtail life forms. It is important to note that about 20% of the assemblage consisted of rare species (i.e. singletons), which may have had dynamics more strongly influenced by other stochastic events rather than the fire. The resistance of springtails found in this study also shows some similarity to other arthropod assemblages in the fire-prone systems of southern Africa. In a savanna habitat, Parr et al. (2004) found ant assemblages to be highly resistant to fire, and similar results have been found for ants in other systems (Friend and Williams, 1996; Anderson and Müller, 2000; Parr et al., 2002; Parr and Andersen, 2008). Other arthropods in the fynbos, such as beetles, have shown similar post-fire responses (Pryke and Samways, 2012). The resistant springtail species were mostly from the euedaphic and epiedaphic groups. Species from the atmobiotic group were more vulnerable to the fire as most were exposed on the vegetation, while euedaphic and epiedaphic species may have survived the fire. Similar results have also been found in studies of forest springtails (Malmström et al., 2009; Greenslade and Smith, 2010). Suggestions from long-term studies indicate that atmobiotic groups tend to be more severely affected by fire than other groups, but gradually recover over time (Malmström, 2012). Because Collembola migrate deeper into the soil during periods of heat or drought (Hopkin, 1997), and as the fire occurred during February, which is the peak of the summer dry period in the fynbos, many species may have survived the fire as they were already deep enough in the soil to avoid the fire. Post-fire recovery may also

depend on species traits related to physiology and dispersal (Gongalsky et al., 2012). However, as the springtail taxonomic diversity of South Africa is only starting to be comprehended (Janion et al., 2011b; Potapov et al., 2011; Janion et al., 2012), it is still unclear which reproductive strategies characterize the fynbos species.

Several species in this study have resilient populations that are able to return relatively quickly to pre-fire abundances or to increase in abundance after fire. Decomposition rate has been shown to vary between litter types in the fynbos (Bengtsson et al., 2012). *Galenia* litter had the highest decomposition rate while *Restio* litter had the lowest. It has been suggested that fire is the major means of nutrient release (Stock and Allsopp, 1992), due to the large variation in decomposition rates found in the fynbos. Boom species and increasers may be responding to nutrient enrichment after the fire, taking advantage of these higher levels of nutrients by reproducing rapidly. In addition, the fire may have also eliminated many springtail predators, allowing these boom species to reach these high population numbers. Our data published earlier (Bengtsson et al., 2011) shows that litters with a high decomposition rate such as *Galenia africana*, which is also very nutrient-rich, have a higher abundance of springtails (see also Leinaas et al., 2015). This relationship also seems to be dependent on the number of years after the fire, thus could explain the extremely high abundance of a few species during the two years after the fire. Nutrient and humidity conditions may be important (see Liu et al., 2012 for an example of the significance of humidity from the region), but may affect species differently, and also depend on both nutrient availability and soil moisture conditions of the two sites at different times. These inter-annual changes in edaphic conditions may have resulted in significant interactions between litter type and year in our study.

High resilience has been found in other arthropods in the fynbos, with most taxa recovering in three years after fire (Pryke and Samways, 2012). In temperate forests, invertebrates were found to be more resilient to single fire events than to repeated fires, with ground-dwelling species showing the lowest resilience (Moretti et al., 2006). In some cases, ants also respond by increases in abundance in response to fire (Parr et al., 2004). Similarly in this study, the majority of species in the Protea site showed an increase in abundance after the fire (32%). Ant assemblages in savannas have returned back to their pre-fire state in as little as eight months after fire (Parr et al., 2004; Frizzo et al., 2012; Andersen et al., 2014). However, for springtails, times to recovery have varied between one and 27 years, with the intensity of the fire having a large



influence on recovery rate (Saestedt, 1984; Driessen and Greenslade, 2004; Malmström et al., 2009; Greenslade and Smith, 2010; Gongalsky et al., 2012; Huebner et al., 2012; Malmström, 2012).

The predominance of resistance and resilience over decline is perhaps not uncommon in fire-prone systems. Which mechanisms underlie the response in springtails in these systems is not clear. They may be linked to the resilience (i.e. the ability to return to the pre-fire state) of the plants characteristic of a given site, which in the fynbos biome is dependent on their life histories (Keeley, 1986; van Wilgen and Forsyth, 1992; Wilson et al., 2015). Sprouters such as *Protea nitida* (which dominated in the *Protea* site) can survive fires and are not severely affected (depending on the fire severity), while non-sprouters (reseeders) such as Ericaceae rely on seed banks to regenerate. Thus, the *Erica* site should take longer to return to its original state before the fire, while the *Protea* site should recover quicker. There is some circumstantial evidence for this in the present study. Abundance seemed to decrease more after the fire in the atmobiotic and epiedaphic groups in the *Erica* site, and also varied more after the fire. The Collembola assemblage may have recovered more quickly in the *Protea* site due to the availability of refugia and the faster post-fire recovery of vegetation (Supplementary material Fig. S9). The availability of refugia (such as remaining vegetation and litter between stones) may play a vital role in the re-colonisation and survival of species, while the quantity and quality of the remaining organic matter may also play an important role (Zaitsev et al., 2016). In addition, litter is thicker in the *Protea* site than in the *Erica* site due to a slower decomposition rate of this vegetation (see Bengtsson et al., 2012), thus creating additional refugia, while the post-fire root system recovery may create deeper nutrient rich micro-refugia, aiding the recovery of Collembola. These refugia may have provided shelter, re-colonisation sites and food availability for springtails immediately after the fire, enabling them to feed and reproduce. Similar observations on the importance of post-fire refugia have been made for ants, spiders, centipedes and crickets (Pryke and Samways, 2012).

## 5. Conclusions

Although the fynbos springtail assemblages had not fully recovered to pre-fire abundance, many species appear to be resistant to or recover rapidly after fires, and the assemblages of both *Protea* and *Erica* sites show evidence of short-term resilience, with relatively rapid return to original conditions. Although additional longer-term and experimental work is required to fully verify these outcomes, the springtail assemblages examined here appear to be similar to ants from fire-prone savanna systems (Parr et al., 2004), and so far as can be ascertained from the higher taxonomic level data, to multiple groups of arthropods in the fynbos (Pryke and Samways, 2012). In consequence, we are unable to reject our hypothesis that these characteristics extend to springtail assemblages, at least over the short-term (ca. four years). Studies on Collembola in other systems such as boreal forests found similar results too, with fire intensity being the most important determinant of survival (Malmström et al., 2009; Gongalsky et al., 2012). Usually fires in the fynbos have a return time of between 10 and 15 years (van Wilgen and 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 and Hensbergen, 1992). This may account for the faster return times documented here than for other springtail assemblages, though noting the short-term nature of our study. Given changing fire regimes (van Wilgen et al., 2010) and the increasing frequency of fires due to human disturbances (Syphard et al., 2009), the system will likely become more dominated by resistant springtail species preferring nutrient rich circumstances

and easily decomposed litters, including invasive species. Similar responses to other disturbance regimes, such as habitat fragmentation, show this may occur in the region (Leinaas et al., 2015), highlighting the importance of considering the biological outcomes of interactions between disturbance drivers.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.apsoil.2016.08.001>.

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