



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://www.elsevier.com/locate/SciVerseScienceDirect)

Pedobiologia - International Journal of Soil Biology

journal homepage: www.elsevier.de/pedobi

Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations

W.P.A. Liu, C. Janion*, S.L. Chown

Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

ARTICLE INFO

Article history:

Received 6 October 2011
 Received in revised form 12 March 2012
 Accepted 17 March 2012

Keywords:

Afforestation
 Alien species
 Cape Floristic Region
 Soil fauna

ABSTRACT

The replacement of indigenous vegetation by commercial alien plantations can strongly affect invertebrate species richness and composition. This has been demonstrated for some invertebrate taxa in the Fynbos vegetation of the Western Cape, but the response of litter-dwelling Collembola has not been documented. Here we compared the richness and abundance of litter-dwelling Collembola assemblages in *Pinus radiata* plantations and in adjacent rehabilitated Cape Flats Sand Fynbos (CFSF) in the Tokai Forest Reserve, Western Cape, South Africa. A total of 48 Collembola morphospecies was identified, of which 14 species were recorded exclusively from the pine plantations, and six exclusively from the CFSF. Abundance and morphospecies richness was higher in the pine plantations than in the CFSF, with 34 morphospecies found in the CFSF, and 42 morphospecies in the pine plantations. Fourteen species were likely invasive taxa, of which eight were found in CFSF, and 13 in the pine plantations. Multivariate analyses indicated significant differences in the assemblages of the two habitat types based on abundance, but using presence–absence data only, no difference was found. Significant relationships were found between springtail richness and abundance and site humidity, which differed between the CFSF (drier) and pine plantation (moister), likely accounting for the differences in richness and abundance among habitat types.

© 2012 Elsevier GmbH. All rights reserved.

Introduction

Located at the south-western tip of Africa, the Fynbos Biome is widely known for its high floral diversity and endemism (Goldblatt 1997; Goldblatt and Manning 2002). Fynbos, the predominant vegetation complex of the biome (Rebelo et al. 2006), is threatened by a variety of direct and indirect anthropogenic factors, including urbanization, agriculture, biological invasions by woody species, nutrient loading, and climate change (Richardson et al. 1996; Rouget et al. 2003; Hannah et al. 2005; Rebelo et al. 2006; Gaertner et al. 2009; Wilson et al. 2009). From the landscape change perspective, alien pine plantations and invasions by pines into natural areas not only have a substantial effect on plant species richness and composition, but they also affect other ecosystem characteristics and functioning profoundly, with the exception perhaps of soil pH and N (Richardson et al. 1992, 1996; Richardson and Cowling 1992; Stock and Allsopp 1992; Richardson and Higgins 1998; Scholes and Nowicki 1998; van Wilgen 2009). The impacts on plant community structure and functioning also translate into significant effects on invertebrate assemblages. By comparison with adjacent Fynbos

vegetation, areas dominated by pines have lower invertebrate richness and abundance, at least in the case of the few groups that have been assessed (Donnelly and Giliomee 1985; Pryke and Samways 2009).

Within the Fynbos vegetation complex many of the vegetation types are considered threatened. In particular, Cape Flats Sand Fynbos (CFSF) is listed as critically endangered mostly owing to its localized occurrence (Cape Town Area only), and the substantial transformation of more than 80% of its original area by urbanization and afforestation (Holmes 2008). The few, small, remnant fragments of CFSF have been accorded considerable conservation priority, and large areas of pine plantations are being removed as part of a long-term rehabilitation programme (e.g. c. 150 ha in the Tokai Forest Reserve) (Rebelo et al. 2006). Despite the conservation significance of the CFSF little is known about its invertebrate fauna by comparison with other vegetation types in the Fynbos biome (e.g. Picker and Samways 1996; French and Major 2001; Botes et al. 2006, 2007; Procheş and Cowling 2006; Pryke and Samways 2009, 2010). Moreover, investigations of the effects of landscape transformation on CFSF seem limited to impacts on vascular plants and on the avifauna (Rebelo et al. 2006; Dures and Cumming 2010). More generally, restricted knowledge of invertebrate responses to landscape transformation is not uncommon for the region. Owing partly to the taxonomic impediment (Samways 2007), and partly

* Corresponding author. Tel.: +27 218083396.
 E-mail address: cjanion@sun.ac.za (C. Janion).

to the significance of insects as pollinators and seed-dispersers in Fynbos (Johnson 1992), investigations tend to be focussed on pollinating insects, ants, and dragonflies (e.g. French and Major 2001; Donaldson et al. 2002; Braschler et al. 2010; Samways and Sharratt 2010), and only occasionally consider other groups (Witt and Samways 2004; Pryke and Samways 2009). Indeed, the less conspicuous soil mesofauna, such as springtails and mites, is largely neglected, despite its widely acknowledged significance in ecosystem functioning (Brussaard et al. 1997; Bengtsson 1998; Behan-Pelletier and Newton 1999; Wardle et al. 2004).

Such a situation applies particularly to the springtails. Although they are widely distributed in virtually all terrestrial habitats (Hopkin 1997), make a significant contribution to soil system functioning (Rusek 1998), and are likely to show significant diversity and endemism in South Africa (Yosii 1959; Coates 1968a,b; Janion et al. 2011a) with concomitant implications for ecosystem functioning (Bengtsson et al. 2011, 2012), detailed ecological studies are lacking, and the diversity of the group in both disturbed and undisturbed Fynbos areas has not been investigated. Therefore, we provide here an assessment of springtail diversity in a Cape Flats Sand Fynbos system and the adjacent areas dominated by managed *Pinus radiata* plantations.

Material and methods

Study site

The study was conducted in Tokai Forest Reserve (TFR) (S34°3.416' E18°25.659'), part of Table Mountain National Park in the Western Cape Province of South Africa. This particular site was chosen largely because, despite being under rehabilitation, it is one of the most extensive remnant patches of CFSF. Most of the other patches are tiny remnants surrounded by urban areas, 'mismanaged' in a variety of ways (Rebelo et al. 2006: 140), and subject to substantial edge effects. The area has a Mediterranean-type climate, with mean daily minimum and maximum monthly temperatures of 7.3 °C and 27.1 °C for July and February, respectively, and a predominantly winter rainfall regime (c. 576 mm year⁻¹, with a peak from May to August, Rebelo et al. 2006). Located on acidic and gray regic sands, the predominant indigenous vegetation type of the TFR is Cape Flats Sand Fynbos, which is characterized by four main plant families, viz. Proteaceae, Restionaceae, Asteraceae (in drier areas) and Ericaceae (in wetter areas), and dominated by dense, relatively tall shrubs (Rebelo et al. 2006). A total of 108 vascular plant species is known from the CFSF, of which one is extinct and three currently exist in cultivation and are being reintroduced into remnant patches (Rebelo et al. 2011). As a consequence of the history of commercial afforestation of the area, remnant patches of CFSF are interspersed among 460 hectares of managed vegetation, predominantly planted *Pinus radiata*, and small patches of cleared areas that are being restored to Sand Fynbos. The reserve has been under the management of South African National Parks (SANParks) since 2005.

Sampling and species identification

Sampling was conducted in mid-winter between 27th July and 26th August 2010. Mid-winter is typically a period of high precipitation and a period of high Collembola activity (Bengtsson et al. 2011). Sampling sites were selected within the lower section of the reserve to minimize elevation differences among sites. A total of eight independent sampling sites was selected: four pine plantation patches (pine habitat) which were planted between 1973 and 1997, and four CFSF patches (CFSF habitat) which have been rehabilitated after pine removal between 1998 and 2007 (Table 1;

Table 1

The year of establishment at each sampling site.

Sampling site	Year of establishment
Pine 1	1996
Pine 2	1973
Pine 3	1995
Pine 4	1997
Cape Flat Sand Fynbos 1	1998
Cape Flat Sand Fynbos 2	2004
Cape Flat Sand Fynbos 3	2007
Cape Flat Sand Fynbos 4	2005

SANParks data). This age variation was unavoidable, as the CFSF sites are critically endangered and are being restored. However, for one of the CFSF sites the age was within a few years of the youngest pine plantations, and we considered age effects much less of a potential confounding factor than the edge effects in smaller, but perhaps older, patches of CFSF elsewhere (see Introduction), as has been found for other taxa (Rebelo et al. 2006, 2011; Dures and Cumming 2010). The largest and smallest distances between sites were 1714 m and 171 m, respectively. Sampling took place approximately once every week and sampling was completed for two to three sites per sampling event. Within each sampling site, two parallel transects were laid out approximately 10 m apart and five litter samples were collected at 10 m intervals along both transects, resulting in 10 samples per site. The sampling for both habitat types was undertaken at least 50 m into the vegetation to eliminate edge effects. Thus, a total of 80 samples was collected (i.e. eight sites with 10 samples in each). Collembola were sampled by taking one liter of surface organic litter (approximately 5 cm in depth). A 1 m² grid was placed over each sampling point, and the sample was collected within the grid to fill the one liter container. All of the organic litter samples within CFSF were collected under *Metalasia muricata*, which was one of predominant indigenous shrubs within the Sand Fynbos patches. Within the pine plantation sites, organic litter samples were collected directly under *P. radiata*.

Ambient temperature and relative humidity were taken in the field approximately 3 cm above the soil surface at the shaded side of each sampling point by using a handheld Vaisala HM32 thermohygrometer (Vaisala, Finland). This resulted in 80 measures of temperature and humidity (40 for each habitat type). In addition, two soil samples were collected haphazardly at two sampling points in each site and were mixed together to form a single sample of 450 g, resulting in a sample size of four for each habitat type. These soil samples were analyzed for soil type, pH, P (Bray and Kurtz 1945), C, N, Mg and Ca by a commercial service provider (BemLab (Pty Ltd.), Somerset West, South Africa).

The litter samples collected for invertebrate extractions were kept cool in an insulated container and transported to the laboratory for extraction within 6 h of collection, to minimize death of the sampled Collembola and the risk of them being consumed by predators such as spiders (Rusek 1998; Hopkin 2007). Collembola were extracted from the litter using Berlese–Tullgren funnel extraction (see Macfadyen 1953). Each sample was extracted individually and the Collembola stored in 99.9% ethanol. Individuals were assigned to morphospecies using external morphological characteristics or to species level, where possible, using European keys (Fjellberg 1998, 2007; Bretfield 1999; Potapov 2001; Hopkin 2007; Bellinger et al. 2011) and information currently being collected by a large project within the Centre of Excellence for Invasion Biology in collaboration with specialists in France, Norway and Sweden (Janion et al. 2011a,b; Potapov et al. 2011). The use of morphospecies enables rapid evaluation of the invertebrate assemblages in question by avoiding the need for complete species identifications. Although the approach has several problems, one of us (CJ) has considerable experience with the Fynbos fauna (e.g. Janion et al.

2011a,b; Potapov et al. 2011), and we have confidence that the large majority (>95%) of the species delimitations refer to single species, even where species-level names for these taxa are not yet available. Similarly, invasive species status was assigned based on whether taxa at the given level of identification are considered typical of Africa or of the Southern Hemisphere generally, or are considered are of European origin using keys available (Fjellberg 1998, 2007; Potapov 2001; Hopkin 2007). All sorting was done by one researcher (WPAL) using a Leica MZ 7.5 microscope, and the species delimitations assessed by a second (CJ). Therefore, the data are comparable between the eight sites. The numbers of individuals for each morphospecies in each site were counted.

Statistical analysis

Sampled-based rarefaction curves for Collembola were assembled for CFSF and pine plantation sites to establish the level of sampling efficiency (EstimateS V8.2, Colwell 2009, <http://viceroy.eeb.uconn.edu/estimates>; Gotelli and Colwell 2001). These curves assess the number of expected species from the known number of observed individuals in the samples (Gotelli and Colwell 2001). The non-parametric Incidence Coverage Estimator (ICE), Michaelis–Menten, Chao 2 and first-order Jackknife richness estimators were selected to estimate the sample size adequacy (Palmer 1990; Colwell and Coddington 1994; Chazdon et al. 1998; Brose 2002). These are known as useful estimators because they are most stable even with small sample sizes (Magurran 2004). Sampling may be considered as sufficient when the sample-based rarefaction curves and the four non-parametric estimators converge closely at the highest observed morphospecies richness (Magurran 2004).

Differences in site morphospecies richness and abundance among sites were examined using a generalized linear model assuming a Poisson distribution with a log-link function, corrected for overdispersion where necessary (implemented in Statistica V. 10.0, StatSoft, Tulsa, Oklahoma). The extent to which CFSF and pine-dominated sites differ in assemblage structure was investigated using routines available in PRIMER V 5.0 2001 (Plymouth Routine in Multivariate Ecological Research, see Clarke and Warwick 2001). The data were double square-root transformed prior to analysis to weight common and rare morphospecies equally. The Bray–Curtis similarity measure was used to construct a similarity matrix among all sites (abundances of morphospecies were summed across the ten samples per site). Cluster analysis was then undertaken using group averaging, and a One-way Analysis of Similarity (ANOSIM) was conducted to determine whether the assemblages differ in structure (Clarke and Warwick 2001). The level of difference among habitat types increases as the significant Global R statistic approaches one. Non-metric multi-dimensional scaling (nMDS) (using 500 random restarts) was used to display the relationships among sampling sites. The analyses were repeated after transformation of the data to presence–absence only to determine the extent to which differences in the assemblages among habitat types could be explained by differences in species richness and identity rather than by variation in abundance among species. For further investigation of the numbers of rare species in the two habitat types, common and rare species were defined as the 25% most abundant and 25% least abundant species, respectively, within the assemblages of each habitat type (the proportion of species method – Gaston 1994).

Soil parameters (pH, C, N, P, Ca and Mg) were compared between the CFSF and pine-dominated habitats using Mann–Whitney *U*-tests, while temperature and relative humidity were compared using a one-way analysis of variance, all implemented in Statistica V.10.0. The relationships between temperature and relative humidity, and species richness and abundance across sites were examined

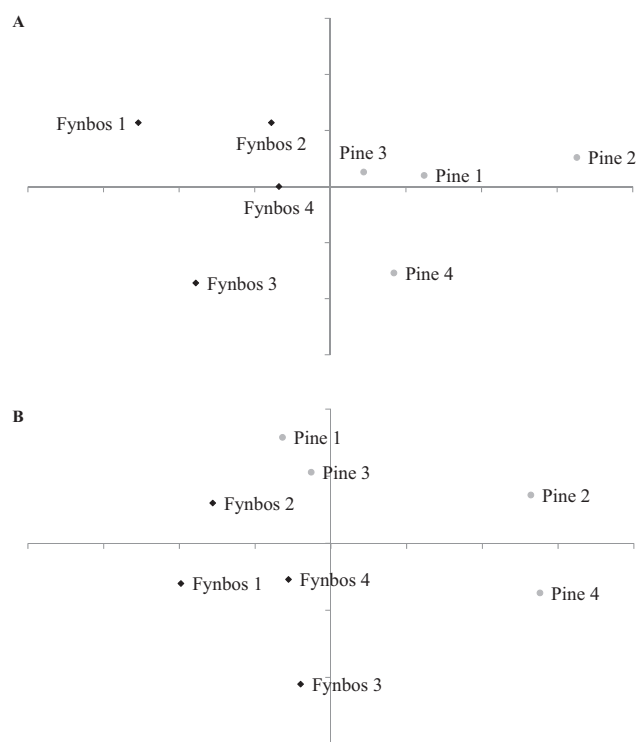


Fig. 1. Non-metric MDS ordination of the sites in each of the sampled habitats based on (A) abundance data (transformed to weight common and rare species equally); among habitat ANOSIM $R=0.531$, $P<0.05$. Stress = 0.06. (B) Based on presence–absence data only; among habitat ANOSIM $R=0.385$, $P>0.05$. Stress = 0.03.

using Pearson's product-moment correlation coefficients (Statistica V.10.0).

Results

A total of 21,728 individuals from 48 Collembola morphospecies was collected from the pine plantation and Cape Flats Sand Fynbos sites in Tokai Forest Reserve (Table 2), of which 13,996 individuals and 42 morphospecies were found in the pine plantations, and 7732 individuals from 34 morphospecies in the CFSF. The sample-based species rarefaction curves and the non-parametric estimators converged closely at the highest observed morphospecies richness for both habitats (Supplementary Figs. S1 and S2), and typically well before the full sample total of 40 for each habitat type, indicating that the sampling for morphospecies richness estimates was sufficient. Of the 48 morphospecies collected, 12 were considered rare (i.e. in the lower abundance quartile), and of these species two were shared among the pine and CFSF habitats (*Dicyrtomina cf. saundersi* and *Seira* sp. 3) (Table 2). Six morphospecies, of which four were rare, were unique to the CFSF, while 14 morphospecies, of which six were rare, were unique to the pine plantation. Mean morphospecies richness differed significantly among sites (Pine: 13.5 ± 0.56 , CFSF: 11.3 ± 0.51 , $\chi^2 = 7.6$, $P=0.006$) as did mean abundance (Pine: 350 ± 48 , CFSF: 193 ± 45 , $\chi^2 = 8.5$, $P=0.004$).

An ANOSIM based on the abundance data revealed that the Collembola assemblages of the CFSF and pine plantation habitats differ significantly (Global $R=0.531$, $P=0.029$) (Fig. 1a), although with some variation within these groups. Pine plantation site 1 had the highest morphospecies richness and abundance of all the sampling sites (Fig. 2a and b), while CFSF 3 had the lowest morphospecies richness (Fig. 2a) and CFSF 1 had the lowest morphospecies abundance (Fig. 2b). Thirteen presumed invasive species were identified, with eight found in the CFSF, and 12 found in the pine plantations (Table 2). Suspected invasive species were found only

Table 2
Abundance of Collembola morphospecies from Cape Flat Sand Fynbos (CFSF) and *Pinus radiata* plantations. The abundance values of the 25% least abundance morphospecies in the samples are indicated in bold.

Order	Family	Species	CFSF	Pine	Invasive/endemic	
Poduromorpha	Hypogastruridae	<i>Ceratophysella cf. denticulata</i>	90	780	Invasive	
		<i>Brachystomella</i> sp.	752	801	?	
	Brachystomellidae	<i>Setanodosa</i> sp.	37	4	Endemic	
		<i>Neanura cf. muscorum</i>	3	23	Invasive	
		<i>Paleonura</i> sp.	0	3	Endemic	
		<i>Micranurida</i> sp.	13	163	?	
	Onychiuridae	<i>Aethiopella cf. flavoantennata</i>	0	1	Endemic	
		<i>Orthonychiurus</i> sp.	0	21	Invasive	
	Tullbergiidae	<i>Mesaphorura cf. macrochaeta</i>	249	69	Invasive	
		<i>Tullbergia</i> sp.	1082	838	?	
	Entombryomorpha	Entomobryidae	<i>Entomobrya cf. multifasciata</i>	279	803	Invasive
			<i>Entomobrya</i> sp. 1	247	465	?
			<i>Entomobrya</i> sp. 2	1	0	?
			<i>Entomobrya</i> sp. 3	2	0	?
<i>Entomobrya</i> sp. 4			0	23	?	
<i>Lepidocyrtus</i> sp. 1			331	1486	?	
<i>Lepidocyrtus</i> sp. 2			0	78	?	
<i>Pseudosinella</i> sp.			35	23	?	
<i>Seira cf. barnardi</i>			0	12	Endemic	
<i>Seira</i> sp. 1			129	253	Endemic	
<i>Seira</i> sp. 2			3	11	Endemic	
<i>Seira</i> sp. 3			2	2	Endemic	
<i>Seira</i> sp. 4			5	19	Endemic	
<i>Seira</i> sp. 5			4	28	Endemic	
Isotomidae			<i>Subisotoma</i> sp.	0	6	?
			<i>Cryptopygus cf. caecus</i>	237	496	?
			<i>Cryptopygus</i> sp. 1	516	15	Endemic
			<i>Cryptopygus</i> sp. 2	714	105	Endemic
			<i>Isotomurus cf. maculatus</i>	0	332	Invasive
			<i>Isotomurus cf. palustris</i>	0	192	Invasive
			<i>Parisotoma</i> sp. 1	1803	721	Endemic
			<i>Parisotoma</i> sp. 2	900	4683	Endemic
			<i>Tomoceridae</i>	<i>Tomocerus cf. minor</i>	0	3
	Neelipleona	Neelidae	<i>Megalothorax</i> sp.	2	164	Invasive
<i>Neelus</i> sp.			0	13	Invasive	
Symphypleona	Mackenziellidae	<i>Mackenziella cf. psocoides</i>	22	0	Invasive	
		<i>Arrhopalites</i> sp.	0	5	?	
	Bourletiellidae	<i>Bourletiella</i> sp.	34	0	?	
		<i>Dicyrtomina cf. ornata</i>	30	22	Invasive	
	Dicyrtomidae	<i>Dicyrtomina cf. saundersi</i>	4	3	Invasive	
		<i>Dicyrtomina</i> sp.	3	0	?	
	Katiannidae	<i>Sminthurinus cf. elegans</i>	0	906	Invasive	
		<i>Sminthurinus</i> sp. 1	59	38	?	
		<i>Sminthurinus</i> sp. 2	30	34	?	
		<i>Sminthurinus</i> sp. 3	0	21	?	
Sminthurididae	<i>Sminthurides</i> sp. 1	7	0	?		
	<i>Sminthurides</i> sp. 2	37	30	?		
	<i>Sphaeridia</i> sp.	70	301	?		
Total		7732	13,996			

in Pine 2, including *Isotomurus cf. maculatus*, *Isotomurus cf. palustris*, *Orthonychiurus* sp. and *Sminthurinus cf. elegans*. The only invasive species that was only found in CFSF was *Mackenziella cf. psocoides*. The high morphospecies diversity found in CFSF 2 was comparable to that of some of the pine sites (Fig. 2). When the ANOSIM was repeated using presence–absence data only, no significant difference was found among the assemblages of the two habitat types (Global $R=0.385$, $P=0.057$, Fig. 1b). Thus, the differences among the habitat types had more to do with the relative abundances of the species present than a clear distinction between assemblage membership in the two habitats.

No significant differences were found in pH, C, N, P, Ca or Mg among the habitat types (Mann–Whitney $U=4.0$ – 8.0 , $P>0.3$ in all cases). By contrast, the habitat types differed significantly in temperature (ANOVA $F_{(1, 78)}=23.4$, $P=0.0001$; Pines 17.2 ± 0.26 °C; CFSF 19.0 ± 0.26 °C, mean \pm S.E.) and relative humidity (ANOVA $F_{(1,78)}=35.3$, $P=0.00001$; Pines $68.5 \pm 1.1\%$; CFSF $59.3 \pm 1.1\%$). Moreover, the two variables were strongly, negatively related across the sites ($r=-0.79$, $P<0.001$). Significant relationships were also found between morphospecies richness and both temperature

($r=-0.24$, $P=0.03$) and humidity ($r=0.33$, $P=0.003$), and abundance and both temperature ($r=-0.22$, $P=0.049$) and humidity ($r=0.26$, $P=0.02$, Fig. 3).

Discussion

Despite the conservation significance of Cape Flats Sand Fynbos (CFSF), few assessments of the diversity of groups other than the vascular plants have been made for this vegetation type, and studies of impacts of land transformation are restricted to vascular plants and birds (Rebelo et al. 2006, 2011; Dures and Cumming 2010). Our assessment found a total richness of 48 springtail morphospecies across both the CFSF and pine plantation, with 34 species in the former and 42 in the latter. Owing to the taxonomic complexity of some groups (e.g. *Seira*, Tullbergiidae), this may be an underestimate, although sampling had clearly gone to completion, and we consider our species-level assignments accurate. A richness of 48 species for a total area of 2 km² is in keeping with that found in other areas (see Petersen and Luxton 1982).

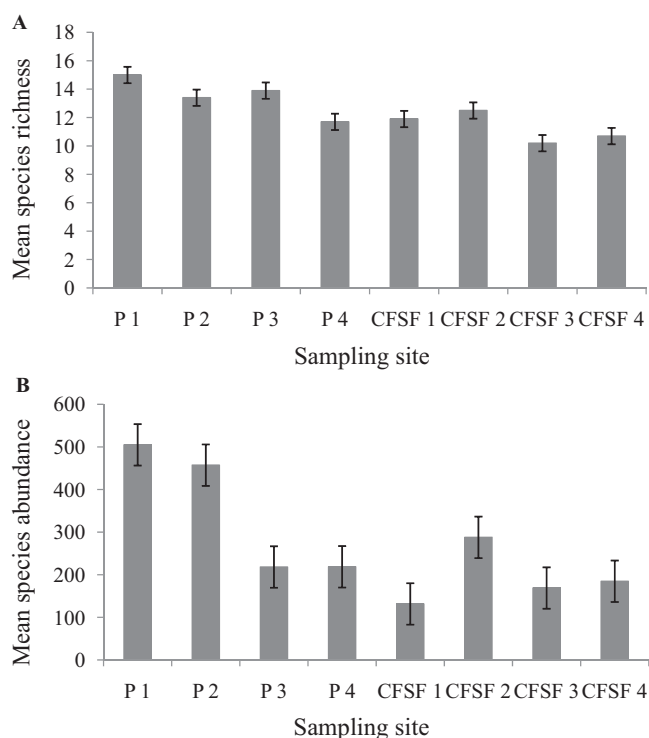


Fig. 2. (A) Mean species richness and (B) abundance per site. The error-bars indicate standard error. P = pine sites, CFSF = Fynbos sites.

The mean site morphospecies richness of 11–14 (CFSF and pine plantation, respectively) is slightly higher than that found for the combined epigaic fauna (i.e. millipedes, scorpions, harvestmen, beetles, ants) examined in the same general area by Pryke and Samways (2010), whilst abundance was very much higher (193–350 individuals in CFSF and pine plantation, respectively) compared with site abundances of less than 100. Springtail site mean richness and abundance is also well within the range found for other groups of epigaic invertebrates investigated in the Fynbos, including spiders, ants, and beetles, and toward the upper end of the values found for the latter taxa (French and Major 2001; Ratsirarson et al. 2002; Witt and Samways 2004; Botes et al. 2006,

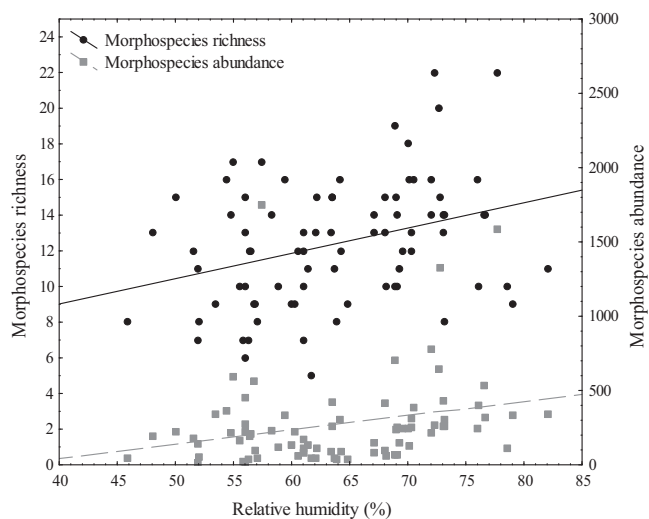


Fig. 3. Variation in morphospecies richness ($r=0.33$; $P<0.05$) and abundance ($r=0.26$; $P<0.05$) were significantly and positively related to relative humidity (%) across the eight sampling sites.

2007). Thus, it is clear that the springtails form an important component of epigaic invertebrate diversity both in the CFSF and pine plantations, as has been recorded elsewhere for this group (Hopkin 1997; Rusek 1998). They are likely also to have much functional significance in these habitats, given that springtails have been shown to have an important role in nutrient cycling elsewhere in the Renosterveld and Fynbos vegetation complexes (Bengtsson et al. 2011, 2012).

By contrast, the extent to which the springtail fauna is restricted to either the location generally, or to the CFSF is not completely clear, mostly because comprehensive investigations of sites elsewhere in the Fynbos biome have yet to be completed (see discussion in Janion et al. 2011a). At least on the local scale, in this study, it is clear that CFSF has six unique morphospecies (*Sminthurides* sp. 1., *Bourletiella* sp., *Dicyrtomina* sp., *Entomobrya* sp. 2, *Entomobrya* sp. 3, *Mackenziella* cf. *psocoides*) (Table 2), of which one is thought to be invasive. However, the significance of this finding is tempered by the fact that the pine plantation included 14 unique morphospecies, of which five are thought to be invasive. Indeed, the invasive species in the pine plantation were typically much more abundant than the invasive species in the CFSF (Table 2).

These results suggested that substantial differences in the assemblages of the two habitat types should be found. Although such a difference was not apparent based only on species identity, it was indeed the case in terms of diversity (i.e. abundance variation among species), and supports other studies showing marked diversity differences among habitat types in the Fynbos, and in the Table Mountain area specifically (French and Major 2001; Ratsirarson et al. 2002; Witt and Samways 2004; Pryke and Samways 2009, 2010). Moreover, the pine plantation springtail assemblage had, on average, both a significantly higher abundance and morphospecies richness than the assemblage in the CFSF. Clearly these differences are not attributable to variation in soil nutrient status because no among-habitat type differences were found in the variables measured (pH, C, N, P, Ca, Mg). Rather, it seems likely that the temperature and relative humidity differences among sites were responsible for the among-habitat type differences in abundance, morphospecies richness and assemblage structure. Springtails typically show substantial sensitivity to desiccation (Choi et al. 2002; Kærsgaard et al. 2004; Chown et al. 2007), and high humidity, low temperature sites would clearly benefit them because both act to reduce the differences in water activity between the organism and its surrounding environment (Wharton 1985; Harrison et al. 1991; Hopkin 1997; Chown et al. 2011). High humidity in the pine plantation is likely associated with the substantial needle litter layer, as is typical of other pine forest sites (Scholes and Nowicki 1998). The favorable conditions in the pine plantation likely also meant a more favorable environment for the suspected invasive species, which reached considerable densities in the case of *Sminthurinus* cf. *elegans*, *Entomobrya* cf. *multifasciata* and *Ceratophysella* sp. (Table 2). Thus, it appears that the non-indigenous vegetation promotes the success of other alien species, an interaction which elsewhere has been known to develop into a substantial synergy known as invasional meltdown (Simberloff 2006). Although this might not turn out to be the case here, the changes in springtail assemblages found, including the increase in the abundance and richness of invasive species, suggest that the invasion of natural Fynbos areas, by pines, as is occurring elsewhere in the region (van Wilgen 2009) may promote invasion by springtail species. Whether this is taking place deserves investigation given the demonstration both in the Fynbos Biome and elsewhere that springtails may substantially affect soil system functioning (Brussaard et al. 1997; Bengtsson 1998; Wardle et al. 2004; Bengtsson et al. 2011, 2012).

In conclusion, the current study has shown that the CFSF houses a diverse assemblage of springtails and that pine plantations are even richer, though they also contain greater richness and

abundance of invasive species. As the particular area (Tokai Forest Reserve) is rehabilitated through the removal of pine plantations, springtail abundance is likely to decline given changing litter levels and abiotic conditions. However, it seems likely that among the springtails the invasive species will be lost, so returning the system perhaps to a state more similar to that of untransformed Fynbos. However, if the rehabilitated areas were invaded by a different plant species which has substantial impacts on both edaphic variables and on humidity and temperature this might not take place. One species that is capable of such transformation is *Acacia saligna* (Yelenik et al. 2004; Le Maitre et al. 2011), and early indications suggest that it might indeed be increasing in abundance in the area (M.A. McGeoch, personal communication). Future work should determine the extent to which this landscape transforming species alters springtail assemblages.

Acknowledgements

We thank South African National Parks for collection permits, Chris Botes for data on site ages, Peter le Roux and Nashreen Williams for assistance, Louis Deharveng and Wanda Weiner for assistance with identification of some of the species, and two anonymous referees for their helpful comments. This work was partly supported by the National Research Foundation and partly by the Working for Water programme.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pedobi.2012.03.002.

References

- Behan-Pelletier, V.M., Newton, G., 1999. Linking soil biodiversity and ecosystem function – the taxonomic dilemma. *Bioscience* 49, 149–153.
- Bellinger, P.F., Christiansen, K.A., Janssens, F., 1996–2011. Checklist of the Collembola of the World. <http://www.collembola.org>.
- Bengtsson, J., 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Appl. Soil Ecol.* 10, 191–199.
- 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 fynbos vegetation, South Africa. *Soil Biol. Biochem.* 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. *J. Biogeogr.* 33, 71–90.
- Botes, A., McGeoch, M.A., Chown, S.L., 2007. Ground-dwelling beetle assemblages in the northern Cape Floristic Region: patterns, correlates and implications. *Aust. Ecol.* 32, 210–224.
- Braschler, B., Mahood, K., Karenzi, N., Gaston, K.J., Chown, S.L., 2010. Realizing a synergy between research and education: how participation in ant monitoring helps raise biodiversity awareness in a resource-poor country. *J. Insect Conserv.* 14, 19–30.
- Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic and available forms of phosphorus in soils. *Soil Sci.* 59, 39–45.
- Bretfield, G., 1999. Synopses on Palaeoartctic Collembola, Vol. 2, Symphypleona. Staatliches Museum für Naturkunde, Göttingen.
- Brose, U., 2002. Estimating species richness of pitfall catches by non-parametric estimators. *Pedobiologia* 46, 101–107.
- Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D.W., Gupta, V.V.S.R., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Soderstrom, B., Tiedje, J.M., Virginia, R.A., 1997. Biodiversity and ecosystem functioning in soil. *Ambio* 28, 563–570.
- Chazdon, R.L., Colwell, R.K., Denslow, J.S., Guariguata, M.R., 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier, F., Comiskey, J.A. (Eds.), *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*. Parthenon, Paris, pp. 285–309.
- Choi, W., Ryoo, M., Kim, J.G., 2002. Biology of *Paronychiurus kimi* (Collembola: Onychiuridae) under the influence of temperature, humidity and nutrition. *Pedobiologia* 46, 548–557.
- 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. *Proc. R. Soc. B* 274, 2531–2537.
- Chown, S.L., Sørensen, J., Terblanche, J.S., 2011. Water loss in insects: an environmental change perspective. *J. Insect Physiol.* 57, 1070–1084.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. PRIMER-E, Plymouth.
- Coates, T.J., 1968a. The Collembola from South Africa – 1: The Genus *Neanura*. *J. Entomol. Soc. S. Afr.* 31, 185–195.
- Coates, T.J., 1968b. The Collembola of South Africa – 2: The Genus *Seira*. *J. Entomol. Soc. S. Afr.* 31, 435–462.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. B* 345, 101–118.
- Colwell, R.K., 2009. EstimateS – statistical estimation of species richness and shared species from samples. Version 8.20. <http://viceroy.eeb.uconn.edu/EstimateSPages/EstimateS.flx>.
- 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. *Conserv. Biol.* 16, 1267–1276.
- Donnelly, D., Giliomee, J.H., 1985. Community structure of epigeic ants in a pine plantation and in newly burnt fynbos. *J. Entomol. Soc. S. Afr.* 48, 259–265.
- Dures, S.G., Cumming, G.S., 2010. The confounding influence of homogenising invasive species in a globally endangered and largely urban biome: does habitat quality dominate avian biodiversity? *Biol. Conserv.* 143, 768–777.
- Fjellberg, A., 1998. The Collembola of Fennoscandia and Denmark. Part I. *Poduromorpha*. *Fauna Entomol. Scand.* 35. Leiden, Brill.
- Fjellberg, A., 2007. The Collembola of Fennoscandia and Denmark. Part II. *Entomobryomorpha* and *Symphyleona*. *Fauna Entomol. Scand.* 42. Leiden, Brill.
- French, K., Major, R., 2001. Effect of an exotic *Acacia* (Fabaceae) on ant assemblages in South African fynbos. *Aust. Ecol.* 26, 303–310.
- Gaertner, M., Breyen, A.D., Hui, C., Richardson, D.M., 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geogr.* 33, 319–338.
- Gaston, K.J., 1994. *Rarity*. Chapman and Hall, London.
- Goldblatt, P., 1997. Floristic diversity in the Cape Flora of South Africa. *Biodivers. Conserv.* 6, 359–377.
- Goldblatt, P., Manning, J.C., 2002. Plant diversity of the Cape Region of Southern Africa. *Ann. Mo. Bot. Gard.* 89, 281–302.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Hannah, L., Midgley, G., Hughes, G., Bomhard, B., 2005. The view from the Cape: extinction risk, protected areas, and climate change. *Bioscience* 55, 231–242.
- Harrison, P.M., Rothery, P., Block, W., 1991. Drying processes in the Antarctic Collembola *Cryptopygus antarcticus* (Willem). *J. Insect Physiol.* 37, 883–890.
- Holmes, P.M., 2008. Optimal ground preparation treatments for restoring lowland Sand Fynbos vegetation on old fields. *S. Afr. J. Bot.* 74, 33–40.
- Hopkin, S.P., 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, New York.
- Hopkin, S., 2007. *A Key to the Collembola (Springtails) of Britain and Ireland*. Forest Stewardship Council, London.
- Janion, C., Bedos, A., Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, H.P., Liu, A., Malmström, A., Porco, D., Chown, S.L., 2011a. Springtail diversity in South Africa. *S. Afr. J. Sci.* 107.
- 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.
- Johnson, S.D., 1992. Plant-animal relationships. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 175–205.
- Kærsgaard, C.W., Holmstrup, M., Malte, H., Bayley, M., 2004. The importance of cuticular permeability, osmolyte production and body size for the desiccation resistance of nine species of Collembola. *J. Insect Physiol.* 50, 5–15.
- Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.-J., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Bignaut, J., Richardson, D.M., 2011. Impacts of invasive Australian acacias: implications for management and restoration. *Div. Distr.* 17, 1015–1029.
- Macfadyen, A., 1953. Notes on methods for the extraction of small soil arthropods. *J. Anim. Ecol.* 22, 65–77.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing Limit, Malden, USA.
- Palmer, M.W., 1990. The Estimation of species richness by extrapolation. *Ecology* 71, 1195–1198.
- Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 39, 288–388.
- Picker, M.D., Samways, M.J., 1996. Faunal diversity and endemicity of the Cape Peninsula, South Africa: a first assessment. *Biodivers. Conserv.* 5, 591–606.
- Potapov, M., 2001. Synopses on Palaeoartctic Collembola, Vol. 3, Isotomidae. In: Dunger, W. (Ed.), *Staatliches Museum für Naturkunde, Göttingen*.
- 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, Ş., Cowling, R.M., 2006. Insect diversity in Cape Fynbos and neighbouring South African vegetation. *Global Ecol. Biogeogr.* 15, 445–451.
- Pryke, J.S., Samways, M.J., 2009. Recovery of invertebrate diversity in a rehabilitated city landscape mosaic in the heart of a biodiversity hotspot. *Landscape Urban Plan.* 93, 54–62.

- Pryke, J.S., Samways, M.J., 2010. Significant variables for the conservation of mountain invertebrates. *J. Insect Conserv.* 14, 247–256.
- Ratsirarson, H., Robertson, H.G., Picker, M.D., Van Noort, S., 2002. Indigenous forests versus exotic eucalypt and pine plantations: a comparison of leaf-litter invertebrate communities. *Afr. Entomol.* 10, 93–99.
- 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.
- Rebelo, A.G., Holmes, P.M., Dorse, C., Wood, J., 2011. Impacts of urbanization in a biodiversity hotspot: conservation challenges in metropolitan Cape Town. *S. Afr. J. Bot.* 77, 20–35.
- Richardson, D.M., Cowling, R.M., 1992. Why is mountain Fynbos invisible and which species invade? In: van Wilgen, B.W., Richardson, D.M., Kruger, F.J., van Hendbergen, H.J. (Eds.), *Fire in South African Mountain Fynbos*. Springer-Verlag, Berlin, pp. 161–181.
- Richardson, D.M., Macdonald, I.A.W., Holmes, P.M., Cowling, R.M., 1992. Plant and animal invasions. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 63–112.
- Richardson, D.M., van Wilgen, B.W., Higgins, S.I., Trinder-Smith, T.H., Cowling, R.M., McKell, D.H., 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodivers. Conserv.* 5, 607–647.
- Richardson, D.M., Higgins, S.I., 1998. Pines as invaders in the southern hemisphere. In: Richardson, D.M. (Ed.), *Ecology and Biogeography of Pinus*. Cambridge University Press, United Kingdom, pp. 450–473.
- Rouget, M., Cowling, R.M., Pressey, R.L., Richardson, D.M., 2003. Identifying spatial components of ecological and evolutionary processes for regional conservation planning in the Cape Floristic Region, South Africa. *Divers. Distrib.* 9, 191–210.
- Rusek, J., 1998. Biodiversity of Collembola and their functional role in the ecosystem. *Biodivers. Conserv.* 7, 1207–1219.
- Samways, M.J., 2007. Insect conservation. A synthetic management approach. *Annu. Rev. Entomol.* 52, 467–487.
- Samways, M.J., Sharratt, N.J., 2010. Recovery of endemic dragonflies after removal of invasive alien trees. *Conserv. Biol.* 24, 267–277.
- Scholes, M.C., Nowicki, T.E., 1998. Effects of pines on soil properties and processes. In: Richardson, D.M. (Ed.), *Ecology and Biogeography of Pinus*. Cambridge University Press, United Kingdom, pp. 341–353.
- Simberloff, D., 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.* 9, 912–919.
- Stock, W.D., Allsopp, N., 1992. Functional perspective of ecosystem. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 241–259.
- van Wilgen, B.W., 2009. The evolution of fire and invasive alien plant management practices in fynbos. *S. Afr. J. Sci.* 105, 335–342.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633.
- Wharton, G.W., 1985. Water balance of insects. In: Kerkut, G.A., Gilbert, L.I. (Eds.), *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 9. Pergamon, Oxford, pp. 565–603.
- Wilson, D., Stock, W.D., Hedderson, T., 2009. Historical nitrogen content of bryophyte tissue as an indicator of increased nitrogen deposition in the Cape Metropolitan Area, South Africa. *Environ. Pollut.* 157, 938–945.
- Witt, A.B.R., Samways, M.J., 2004. Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *Afr. Entomol.* 12, 89–95.
- Yelenik, S.G., Stock, W.D., Richardson, D.M., 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restor. Ecol.* 12, 44–51.
- Yosii, R., 1959. Collembola fauna of the Cape Province, with special reference to the genus *Seira* Lubbock. *Seto. Mar. biol. Lab.*, 1–23, Special Publ. June 1959.