The regeneration of soil micro-arthropod assemblages in a rehabilitating coastal dune forest at Richards Bay, South Africa

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Abstract

The structure and composition of the soil micro-arthropod communities of five postmining rehabilitating sites (between 1 and 24 years after rehabilitation) are compared with that of an undisturbed dune forest benchmark. We extracted soil micro-arthropods (Acari and insects) with a modified Berlese–Tullgren funnel and used soil carbon, calcium, potassium, magnesium, nitrogen, sodium, phosphorous and acidity (pH) as explanatory variables of micro-arthropod community composition. Acari accounted for the majority of all the micro-arthropods (between 65 and 97% of the sample) at the different sites. Density, richness, diversity and composition showed significant differences between the unmined benchmark site and the rehabilitating sites for both insects and Acari, with weak habitat-age related patterns. Canonical Correspondence Analysis suggests that differences between samples from regenerating sites and those from the benchmark sites slowly decrease with increasing regeneration age, but that community composition is only weakly related to soil properties. Our results suggest that coastal dune forest rehabilitation could give rise to the regeneration of micro-arthropod assemblages, but it may take a long time. Therefore, potential limiting factors for community regeneration need to be identified to improve the chances for successful restoration.

Key words: community composition, mining, restoration, soil organisms

Résumé

On compare la structure et la composition des communautés de micro-arthropodes du sol dans cinq sites en voie de réhabilitation après des activités minières (de 1 à 24 ans après la fin des activités) avec celles d'une dune forestière intacte qui sert de référence. Nous avons extrait des micro-arthropodes (acariens et insectes) du sol au moyen d'un entonnoir Berlese–Tullgren modifié et nous avons utilisé le carbone, le calcium, le potassium, le magnésium, l'azote, le sodium, le phosphore et l'acidité (pH) du sol comme variables pour expliquer la composition de la communauté de micro-arthropodes.

Les acariens composaient la majorité de tous les micro-arthropodes (entre 65 et 97% des échantillons) sur les différents sites. La densité, la richesse, la diversité et la composition montraient des différences significatives entre le site de référence et les sites en voie de réhabilitation, pour les insectes comme pour les acariens, avec de faibles schémas de liens âge-habitat. Une Analyse de Correspondance Canonique a suggéré que les différences entre les échantillons venant des sites en voie de réhabilitation et le site de référence diminuent lentement avec la durée de la réhabilitation, mais que la composition des communautés n'est que peu affectée par les propriétés du sol. Nos résultats suggèrent que la réhabilitation de dunes forestières côtières pourrait entraîner la régénération d'assemblages de micro-arthropodes mais que cela peut prendre beaucoup de temps. C'est pourquoi il faut identifier les facteurs susceptibles de limiter la régénération des communautés afin d'augmenter les chances d'une restauration réussie.

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Introduction

Restoration efforts throughout the world are directed at recovering ecosystems typical of the region prior to man-induced disturbance (Greenslade & Majer, 1993; Koehler, 1998, 2000; Majer & Nichols, 1998; Frouz *et al.*, 2001). This is also true for a cordon of coastal dune forests in

northern KwaZulu-Natal, South Africa, where the mining for heavy minerals (zircon, rutile and ilmenite) is followed by a rehabilitation program directed at the regeneration of an indigenous dune forest typical of the region. Here mining involves the removal of all vegetation and the centrifugation of the sand that makes up these dunes, thereby destroying the forest substrate.

The postmining rehabilitation of these dunes, which started in 1978, has given rise to the development of a series of regenerating sites of known age (van Aarde, Ferreira & Kritzinger, 1996a). Studies on small mammals, millipedes, dung beetles, birds, and trees (van Aarde *et al.*, 1996a,b; van Aarde, Smit & Claassens, 1998; Kritzinger & van Aarde, 1998; Davis *et al.*, 2003) living on these dune forests showed that species composition of assemblages change with regeneration age and that the similarity between the species assemblages of rehabilitating and the undisturbed benchmark habitats increased with age. The chemical properties of the soils here also changed with an increase in regeneration age (van Aarde *et al.*, 1998). None of the studies conducted here until now accounted for the soil micro-biota, which may be the basis of terrestrial ecosystem functioning (Mummey, Stahl & Buyer, 2002; Salamanca, Raubuch & Joergensen, 2002). We considered this a shortcoming as these organisms play important roles in soil formation, plant establishment, transformation of soil organic matter and nutrient cycling (Maraun, Visser & Scheu, 1998; Wardle *et al.*, 1999; Bird, Coulson & Crossley, 2000). Subterranean micro-arthropods also help in the decomposition of organic matter, the structuring of the soil, the dispersal of micorrhizal fungi, and are part of subterranean food webs (Eisenbeis & Wichard, 1987; Coleman & Crossley, 1996; Maraun *et al.*, 1998; Bird *et al.*, 2000; Koehler, 2000). In spite of these apparently crucial roles that micro-arthropods play in ecosystem function, relatively few studies have made use of micro-arthropod assembly characteristics to evaluate the success of rehabilitation programs (Greenslade & Majer, 1993; Koehler, 2000; Frouz *et al.*, 2001; Wanner & Dunger, 2002).

Micro-arthropods are unique in the sense that they essentially live in their resources. Consequently, many studies have found that community structure, abundance and diversity of soil micro-arthropods are influenced by the availability of organic matter, substrate quality, concentrations of macro- and micro-nutrients, and age and biodiversity of the rehabilitating habitat (Loranger *et al.*, 1998; Majer & Nichols, 1998; Wardle *et al.*, 1999; Koeh-

ler, 2000; Radea & Arianoutsou, 2000; Frouz *et al.*, 2001; Wanner & Dunger, 2002).

In the present study, we relate changes in the abundance, diversity and composition of soil micro-arthropod assemblages across a sere of postmining rehabilitating coastal dune forests to changes in the chemical properties of the soils in which they live (i.e. a gradient analysis). The sere of rehabilitating dune forests form a chronosequence, with habitats (stands) of successive postmining age situated in close proximity to each other. We furthermore compare these micro-arthropod communities with those of a benchmark (unmined and undisturbed) dune forest, to establish whether rehabilitation is associated with the regeneration of typical dune forest micro-arthropod assemblages.

Materials and methods

Study sites

The study was conducted using soil samples collected from the coastal dunes of northern KwaZulu-Natal, South Africa (Fig. 1). Five postmining rehabilitating sites ranging in age from 1 to 24 years, and one unmined and relatively undisturbed dune forest served as sampling sites.

The study area is situated between Richards Bay (28°43′S, 32°12′E) and the Mapelane Nature Reserve (32°25′S, 28°27′E) and has been described by van Aarde *et al.* (1996a). The climate is humid and hot, and the mean annual rainfall is 1292 mm (van Aarde *et al.*, 1996b). Soils are sandy with little vertical differentiation (van Aarde *et al.*, 1996b). We designated each rehabilitating sampling site as a 'stand', which is an area of rehabilitating dune forest where all patches are of equal postmining regeneration age. The rehabilitating sampling sites vary, from young to old, from an indigenous grassland (stands 7 and 8), to a shrubland dominated by *Acacia kosiensis* (P.P. Swartz) with little undergrowth (stand 5), to an *A. kosiensis* dominated woodland with emerging indigenous forest tree species (stands 3 and 1). The benchmark site (Sokhulu) is a relatively undisturbed dune forest typical of the area, with a mixture of various indigenous tree, shrub and climber species. Further details on the sampling sites are provided in Table 1 and by van Aarde *et al.* (1996b).

Sampling of soil for micro-arthropods

Sampling was carried out from 13 to 21 November 2002. Five 2 × 2 m quadrates were randomly laid out in each site
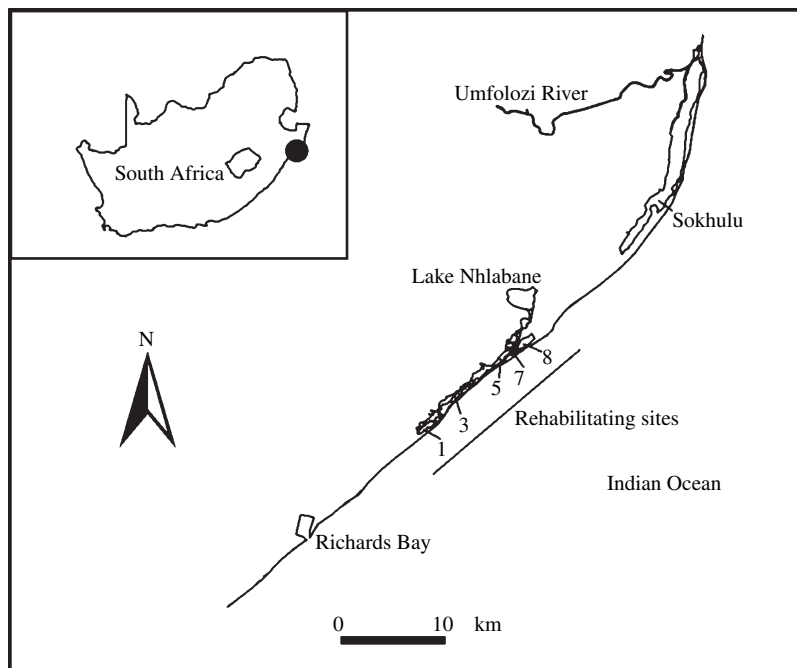
Fig 1 A map showing the location of the five rehabilitating sites (stand 1, 3, 5, 7 and 8) and the relatively undisturbed benchmark site (Sokhulu) from where soil samples were collected as part of the present study

Table 1 A qualitative description of the substrate characteristics of the sites from which samples were collected

Sites	Site age (years)	Substrate characteristics
Stand 8	1	Sand dune with no horizon differentiation and a thin litter layer derived from annual grasses
Stand 7	2	Sand dune with no horizon differentiation and a thin litter layer derived mainly from annual indigenous grasses
Stand 5	10	Sandy soil with a thin organic layer and litter cover from *Acacia kosiensis* leaves and twigs
Stand 3	18	Sandy soil with a thin organic layer and a large amount of litter derived from *A. kosiensis* leaves and dead branches and climbers
Stand 1	24	Sandy soil with a substantial organic layer, and a large amount of litter derived from *A. kosiensis* leaves and dead branches, lianas and other indigenous woody species. Partly decomposed logs of dead *A. kosiensis* are also the characteristic of the stand. Many dead snail shells are found scattered around the stand
Sokhulu	Unknown	Sandy soil with a deep organic layer. The litter layer is composed of the leaves and branches of various indigenous tree and shrub species. We observed many dead snail shells, in various stages of decomposition, scattered widely around the stand

and within each of these two soil samples were taken using a soil corer (volume = 1000 cm^3). The soil samples were transported and then stored at 5–10°C until processed at the University of Pretoria. Soil micro-arthropods were extracted over 7 days using a modified Berlese-Tullgren funnel (Woolley, 1982). A 60 W incandescent bulb, with brightness controlled by a rheostat, was used as a heat source at the top of the funnel. A gradual increase in the

brightness, and hence the temperature, forced the micro-arthropods to the bottom of the soil column, from where they were collected in a vial with 70% ethanol alcohol.

An optical microscope (30–45× magnification) was used to sort the extracted micro-arthropods. A size 00 paint-brush and flattened dissecting needle were used to remove the organisms from the mixture of soil and alcohol. Mites, except Oribatida, were cleared using 90% lactic acid and mounted in a PVA medium for identification (Krantz, 1978). Insects were identified to order level, and experts at the Agricultural Research Council in Pretoria and Bloem-fontein, South Africa, identified representatives of the Acari to family level.

Sampling of soil for chemical analyses

Six soil samples were taken from within each of the five random quadrates and thoroughly mixed. The bulk sample was air-dried on the day of sampling and from this a subsample of 3 kg soil was taken for chemical analysis. The procedures described by The Non-Affiliated Soil Analysis Working Committee (1990) was used to determine levels of all soil chemicals and physical properties. In short, the percent carbon (C) was deter-mined by the Walkley–Black method, the total nitrogen (N) by the Kjeldahl method of digestion by sulphuric acid, extractable phosphorous (P) by the P-Bray extrac-tion method, the exchangeable cations calcium (Ca) and magnesium (Mg) by atomic absorption spectroscopy, and potassium (K) and sodium (Na) by flame emission spectroscopy.

Data analysis

The Acari were identified to family level and the insects to order level. Because of this, the numerical analysis of the two communities was conducted separately. CANOCO^{TM} 4.5 for Windows (ter Braak & Smilauer, 2002) was used for the ordination of the different rehabilitating and benchmark sites based on the association of micro-arthropod community composition to soil chemical prop-erties. Soil chemical variables used in the Canonical Correspondence Analysis (CCA) ordination were selected based on the result of forward selection and correlations among them. Abundance data of the micro-arthropods were log$_e$ transformed, while the soil chemical variables were standardized to a mean of zero and a standard deviation of one to make the eigenvalues comparable (ter

Braak, 1986; Legendre & Legendre, 1998). The CCA pro-cedure includes a Monte Carlo type permutation test to test for significant associations between the environment and community composition (ter Braak & Smilauer, 2002).

The equation $H' = -\sum p_i \ln (p_i)$, where p_i is the pro-portion of the total count (or biomass) for the ith taxa, was used to calculate the Shannon–Wiener diversity index (H') using PRIMER^{TM} V5.0 (Clarke & Warwick, 2001). SPSS for Windows V11.0 (SPSS Inc., Chicago, IL, USA) was used for one-way analysis of variance (ANOVA) with Tukey's HSD test for *post hoc* comparisons (Sokal & Rohlf, 1995). The index was checked for uniformity of variance by Bartlett's test for equal variances, and we used the Kolmogorov–Smirnov test for normality (Sokal & Rohlf, 1995).

Results

Community structure and abundance: Acari

The Acari accounted for 83% of the total soil micro-arthropods found in all six sites and between 65–97% of the micro-arthropods at each site. Twenty families of Acari were identified and none of these occurred at all the sites. The Rhodacaridae occurred at five sites, Tectocepheidae at four sites, the Stigmaeidae and Uropodidae at three sites each, the Carabodidae, Galumnidae, Scheloribatidae and Trombiculidae at two sites each and the remaining 12 were encountered at only one site. Cross-taxon total densities were unequally distributed amongst the sites. Total density on the oldest rehabilitating site and Sokhulu (an average of 1320 and 1060 individuals m^{-2}, respect-ively), was more than three times the density of the next most abundant site (the 1-year-old site, with 320 indi-viduals m^{-2}). The rest of the sites had between 200 and 240 individuals m^{-2}. Families shared between the reha-bilitating sites and the benchmark site increased margin-ally with an increase in regeneration age, from one in the youngest site to three each in the two oldest sites.

Community structure and abundance: insects

Insect orders accounted for 17% of the micro-arthropods found at the six sites and 3–45% of the micro-arthropods at each site. Eight orders were found across all the sites, but none occurred on all the sites. The rehabilitating sites all had either two or three orders, with no discernible pattern in occurrence. Just over half the orders (five of eight) occurred on the benchmark site. Three of the eight orders

(Hymenoptera, Lepidoptera and Thysanoptera) were associated with stands <10 years of age. Collembola was the most common taxon on all sites except the youngest. The highest total insect density (average of 380 individuals m^{-2}) was recorded on the benchmark site, followed by the second oldest rehabilitating site (120 individuals m^{-2}). The rest of the sites all ranged between an average of 40 and 60 inividuals m^{-2}, with lowest densities recorded at stands 5 and 1. The number of insect orders shared with the benchmark site ranged between one and three for the rehabilitating sites, but this showed no age-related pattern.

Gradient analysis: Acari

The term gradient analysis is used here to mean relating the taxa composition of the various sites with soil properties. CCA with forward selection (ter Braak & Verdonschot, 1995; ter Braak & Smilauer, 2002) identified K, C, N and Mg as the four most important variables associated with community structure and composition of the Acari. However, only K was significantly correlated with community composition ($P < 0.05$, 499 unrestricted permutations). Potassium was also highly correlated with C, Mg, K, and Na (all $R > 0.96$, $P < 0.05$); K therefore adequately represented the association of all these variables with community structure (ter Braak & Smilauer, 2002). Potassium, N, P and pH were therefore used as the explanatory environmental variables in the triplot CCA ordination of Acari taxa and the different sites.

The eigenvalues of the first and second axes for the ordination of Acari families and environmental characteristics were 0.745 and 0.488, respectively. The first two axes cumulatively explained 57.9% (35.4 and 22.5% for axes 1 and 2, respectively) of the variance in families and 68% (41.1–26.9% for axes 1 and 2, respectively) of the variance in family–environment relations. Potassium ($R = -0.91$ on the first axis), and pH ($R = 0.93$ on the second axis) contributed the most to the gradient on the CCA plot. The contribution of both the first and all canonical axes were significant ($P < 0.05$, 499 unrestricted permutations).

The family points of Epicriidae, Gymnodamaeidae, Haplozetidae, Oppiidae, Pachylaelapidae, Plateremaeidae and Polyaspidae associated closely with Sokhulu (i.e. they had a greater chance to be found there and had a higher relative abundance there than in the other sites) (Fig. 2). These families are associated with relatively high values of

K, N and pH, and low values of P. The family points of the Acaridae and Ceratozetidae coincided with stand 7 (mostly high pH and low P); while those for the Rhagidiidae and Oribatulidae overlapped with stand 8 (high P, low N, K, and pH) (Fig. 2).

Gradient analysis: insects

Forward selection with CCA showed that among the eight soil chemical properties measured, none had a significant influence on the community ordination of the insect taxa ($P > 0.05$, 499 unrestricted permutations). The four most important soil variables used in the CCA ordination were Mg, N, P and pH.

For the CCA ordination of the insect orders (Fig. 3), the eigenvalues of axes 1 and 2 were 0.564 and 0.352, respectively. The first two axes cumulatively accounted for 58% (35.7 and 22.3% for axes 1 and 2, respectively) of the variance in orders and 68.6% (42.2 and 26.4% for axes 1 and 2, respectively) of the variance in order–environment relations. The soil chemical variables determining the gradients in the CCA diagrams were pH for axis 1 ($R = -0.74$) and P for axis 2 ($R = 0.39$). The contribution of both the first and all canonical axes were not significant ($P > 0.05$, 499 unrestricted permutations).

The order points of Collembola, Diplura, Diptera and Hemiptera appeared to cluster around Sokhulu (associated with intermediate levels of P, Mg, and N), while the Lepidoptera associated with stand 8 and the Thysanoptera with stand 7 (Fig. 3).

Diversity: Acari

Family diversity (H') of Acari did not differ significantly between stands ($F_{5,29} = 1.88$, $P > 0.05$), although the diversity in the undisturbed forest (Sokhulu) was almost twice more than on the next most diverse stand (Table 2). The mean family richness of Sokhulu differed significantly ($F_{5,29} = 2.98$, $P < 0.05$) from that in stands 5 and 7, but not from that of the other rehabilitating stands. In total, fewer families were recorded on the regenerating sites than on the benchmark site, with twice as many families on the benchmark site (Sokhulu, twelve families) than on the 1-year-old site (stand 8). Richness and diversity both appeared to decline from relatively high values in the youngest stand, before increasing again as the sites grew older (Table 2).
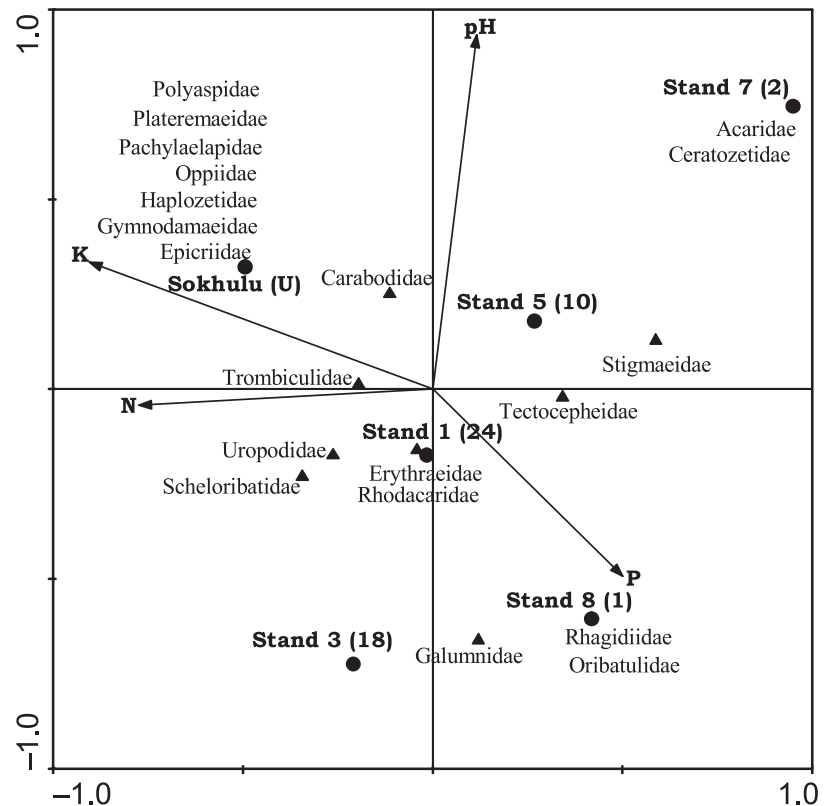
Fig 2 A Canonical Correspondence Analysis ordination triplot of soil Acari families (▲), soil chemical properties (→), and sites (●) in the plane of axes 1 (horizontal) and 2 (vertical). The number following the site name in parenthesis is the age of the site, U means unknown age. The eigenvalues of axes 1 and 2 are 0.745 and 0.488, respectively

Diversity: insects

The Shannon–Wiener diversity index of the benchmark habitat was significantly different from those of stands 1, 5 and 7 ($F_{5,29} = 2.972$, $P < 0.05$), but not from those of the other regenerating sites (Table 2). There were no significant differences among the rehabilitating stands in terms of Shannon-Wiener diversity index and no apparent age-related pattern (Table 2). The benchmark habitat (Sokhulu) had significantly higher mean order richness than stands 1 and 5 ($F_{5,29} = 3.25$, $P < 0.05$), but did not differ from the other rehabilitating stands. Insect order richness for the rehabilitating sites did not differ significantly from one another.

Discussion

The densities of soil micro-arthropods increased with an increase in regeneration age, but not monotonically. The youngest rehabilitating site had the highest total density after Sokhulu and stand 1, most likely because these organisms were inoculated when topsoil, collected from cleared forest as part of the rehabilitation process, was

spread onto the newly rehabilitated sites (van Aarde *et al.*, 1996a). The subsequent decrease in the abundances of micro-arthropods at the other rehabilitating sites may be because of the exhaustion of the soil organic matter through time that may not have been replaced by the establishing plant community.

The overall density of micro-arthropods in our study was considerably lower than those recorded in dry forest (63,000 individuals m^{-2}) and in savanna regions (32,000 individuals m^{-2}) (Noti, André & Dufrêne, 1996). This may be ascribed to seasonal differences in the time of sampling as soil micro-arthropod density varies considerably between seasons (Wardle *et al.*, 1999; Bird *et al.*, 2000; Haimi, Fritze & Moilanen, 2000; Radea & Arianoutsou, 2000).

Diversity trends were similar to those for abundances – high taxa richness on the undisturbed site, and decreasing taxa richness with increasing regeneration age on the rehabilitating sites (Table 2). The decrease on the rehabilitating sites was not monotonic, indicating taxa replacement and turnover in the stands at various rehabilitation stages (Frouz *et al.*, 2001). The rate and sequence in which benchmark taxa appear in the
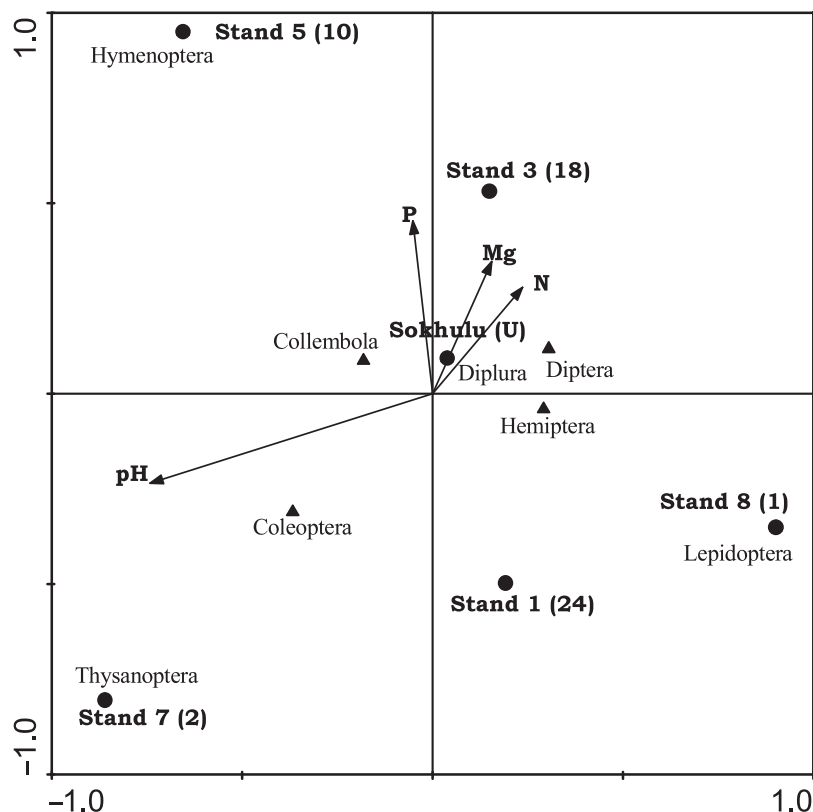
Fig 3 A Canonical Correspondence Analysis ordination triplot of soil insect orders (▲), soil chemical properties (→), and sites (●) in the plane of axes 1 (horizontal) and 2 (vertical). The number following the site name in parenthesis is the age of the site, U means unknown age. The eigenvalues of axes 1 and 2 are 0.564 and 0.352, respectively

Sites	Age in years	Shannon–Wiener diversity index (H')	Mean number of families or orders	Total number of families or orders
Acari				
Stand 8	1	0.577 ± 0.2	2.0 ± 0.4[ab]	6
Stand 7	2	0.277 ± 0.2	1.2 ± 0.4[b]	4
Stand 5	10	0.413 ± 0.2	1.2 ± 0.5[b]	4
Stand 3	18	0.438 ± 0.3	1.8 ± 0.5[ab]	4
Stand 1	24	0.761 ± 0.2	2.4 ± 0.5[ab]	5
Sokhulu	Unknown	1.276 ± 0.4	4.8 ± 1.6[a]	12
Insects				
Stand 8	1	0.139 ± 0.1[ab]	0.6 ± 0.4[ab]	3
Stand 7	2	0[b]	0.6 ± 0.2[ab]	3
Stand 5	10	0[b]	0.4 ± 0.2[b]	2
Stand 3	18	0.139 ± 0.1[ab]	0.8 ± 0.4[ab]	3
Stand 1	24	0[b]	0.4 ± 0.2[b]	2
Sokhulu	Unknown	0.561 ± 0.2[a]	2 ± 0.5[a]	5

Table 2 Mean Shannon–Wiener diversity index (H') and taxon richness (±SE), and total taxon richness for Acari (families) and insects (orders) on the rehabilitating (stands 1, 3, 5, 7 and 8) and benchmark (Sokhulu) sites. Mean values within a column followed by different letters differed significantly. Shannon–Wiener diversity of Acari did not differ significantly among sites

rehabilitating sites suggest that community re-assembly is occurring, but that colonization potential probably differs between insects and Acari.

Surprisingly, soil chemical and physical properties were only weakly associated with community composi-tion of either the Acari or insects. Potassium (statistically significant), N, P and pH (to some extent, but none significant) partly explained Acari abundance and com-position, and none of the soil variables were related to insect composition. Other biotic and abiotic factors must

thus be more important in determining community organization than at first thought. For instance, soil moisture, amount and type of litter, the type of humus, the vegetation type and the time elapsed during the storage of the top soil (Loranger *et al.*, 1998; Koehler, 2000; Hasegawa, 2001; de Goede & Brussaard, 2002; Smolander & Kitunen, 2002) may all affect abundance, and thus community structure. Furthermore, the presence of suitable logs may be an important factor for the re-colonization of some micro-arthropod taxa (Majer *et al.*, 1984).

Nevertheless, the CCA ordination for Acari showed that the community composition of the three oldest rehabilitating sites was more similar to the undisturbed site than the two youngest sites (Fig. 2). This suggests that rehabilitation of these dune forests is associated with the regeneration of soil micro-arthropod communities, although the effect of site age is not very strong. For insects, the separation between the different sites was less clear, but again the older rehabilitating sites were more similar to the benchmark than the rest (Fig. 3). The differences in the response of Acari and insects to rehabilitation indicate that it is not possible to generalize the influence of biotic and abiotic factors on different community assemblages.

Generally, our results indicate that macro-arthropod community structure on rehabilitating sites are slowly becoming more similar to that of communities on the benchmark site as the postmining regeneration age increases. Furthermore, whatever changes occur in community structure are probably not governed by soil chemical and physical properties. Although the present study cannot be considered exhaustive, it does suggest that community regeneration is slow. No doubt rehabilitation is a gradual process. The assessment of micro- and meso-fauna community regeneration may thus entail frequent and long-term monitoring (Greenslade & Majer, 1993; Koehler, 1998, 2000; Majer & Nichols, 1998).

Still, the current limitations on community regeneration need to be explained and we suggest that this should be further investigated. This type of information is important, because it will assist in management decision-making. For example, either colonization rate (Greenslade & Majer, 1993) or substrate quality (Frouz *et al.*, 2001) may turn out to be a bottleneck, which will necessitate different approaches – soils may be inoculated to assist colonization, but inoculation will be ineffective if there is something amiss in the substrate itself.

References

VAN AARDE, R.J., FERREIRA, S.M. & KRITZINGER, J.J. (1996a) Successional changes in rehabilitating coastal dune communities in northern KwaZulu-Natal, South Africa. *Lands. Urban Plan.* **34,** 227–286.

VAN AARDE, R.J., FERREIRA, S.M., KRITZINGER, J.J., VAN DYK, P.J., VOGT, M. & WASSENAAR, T.D. (1996b) An evaluation of habitat rehabilitation on coastal dune forests in northern KwaZulu-Natal, South Africa. *Restor. Ecol.* **4,** 334–345.

VAN AARDE, R.J., SMIT, A-M. & CLAASSENS, A.S. (1998) Soil characteristics of rehabilitating and un-mined coastal dunes at Richards Bay, KwaZulu-Natal, South Africa. *Restor. Ecol.* **6,** 102–110.

BIRD, S., COULSON, R.N. & CROSSLEY G.A. Jr, (2000) Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. *For. Ecol. Manag.* **131,** 65–80.

TER BRAAK, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67,** 1167–1179.

TER BRAAK, C.J.F. & SMILAUER, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide*. Software for Canonical Community Ordination (version 4.5). Micro Computer Power, Ithaca, NY, U.S.A.

TER BRAAK, C.J.F. & VERDONSCHOT, F.M. (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat. Sci.* **57,** 1015–1621.

CLARKE, K.R. & WARWICK, R.M. (2001) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation.* (2nd edn). PREMER-E Ltd, Plymouth.

COLEMAN, D.C. & CROSSLEY, D.A. (1996) *Fundamentals of Soil Ecology*. Academic Press, London.

DAVIS, A.L.V., VAN AARDE, R.J., SCHOLTZ, C.H. & DELPORT, J.H. (2003) Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and un-mined dune forest. *Restor. Ecol.* **11,** 29–42.

EISENBEIS, G. & WICHARD, W. (1987) *Atlas on the Biology of Soil Arthropods.* Springer-Verlag Berlin Heidelberg, Germany.

FROUZ, J., KEPLIN, B., PIŽL, V., TAJOVSKÝ, K., STARÝ, J., LUKEŽOVÁ, A., NOVÁKOVÁ, A., BALÍK, V., HÁNEçL, A., MATERNA, J., DÜKER, C.,

CHALUPSKÝ, J., RUSEK, J. & HEINKELE, T. (2001) Soil biota and upper soil layer development in two contrasting post-mining chronosequences. *Ecol. Eng.* **17**, 275–284.

DE GOEDE, R.G.M. & BRUSSAARD, L. (2002) Soil zoology: an indispensable component of integrated ecosystem studies. *Eur. J. Soil Biol.* **38**, 1–6.

GREENSLADE, P. & MAJER, J.D. (1993) Recolonization by Collembola of rehabilitated bauxite mines in Western Australia. *Aust. J. Ecol.* **18**, 385–394.

HAIMI, J., FRITZE, H. & MOILANEN, P. (2000) Responses of soil decomposer animals to wood-ash fertilization and burning in a coniferous forest stand. *For. Ecol. Manag.* **129**, 53–61.

HASEGAWA, M. (2001) The relationship between the organic matter composition of a forest floor and the structure of soil arthropod community. *Eur. J. Soil Biol.* **37**, 281–284.

KOEHLER, H. (1998) Secondary succession of soil meso-fauna: a thirteen-year study. *Appl. Soil Ecol.* **9**, 81–86.

KOEHLER, H.M. (2000) Natural regeneration and succession – results from a 13 years study with reference to meso-fauna and vegetation, and implications for management. *Lands. Urban Plan.* **51**, 123–130.

KRANTZ, G.W. (1978) *A Manual of Acarology*. 2nd edn. Oregon State University Book Store, Inc., Corvallis.

KRITZINGER, J.J. & VAN AARDE, R.J. (1998) The bird communities of rehabilitating coastal dunes at Richards Bay, KwaZulu-Natal. *S. Afr. J. Sci.* **94**, 71–78.

LEGENDRE, P. & LEGENDRE, L. (1998) *Numerical Ecology.* (2nd English edn). Elsevier Science B. V., Amsterdam, The Netherlands.

LORANGER, G., PONGE, J.F., BLANCHART, E. & LAVELLE, P. (1998) Influence of agricultural practices on arthropod communities in a vertisol (Marinique). *Eur. J. Soil Biol.* **34**, 157–165.

MAJER, J.D. & NICHOLS, O.G. (1998) Long-term recolonization patterns of ants in Western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. *J. Appl. Ecol.* **35**, 161–182.

MAJER, J.D., DAY, J.E., KABAY, E.D. & PERRIMAN, W.S. (1984) Recolonization by ants in bauxite mines rehabilitated by number of different methods. *J. Appl. Ecol.* **21**, 355–375.

MARAUN, M., VISSER, M. & SCHEU, S. (1998) Oribatid mites enhance the recovery of the microbial community after a strong disturbance. *Appl. Soil Ecol.* **9**, 175–181.

MUMMEY, D.L., STAHL, P.D. & BUYER, J.S. (2002) Microbial biomarkers as an indicator of ecosystem recovery following surface mine reclamation. *Appl. Soil Ecol.* **614**, 1–9.

NOTI, M.I., ANDRÉ, H.M. & DUFRÊNE, M. (1996) Soil oribatid mite communities (Acari: Oribatida) from high Shaba (Zaïre) in relation to vegetation. *Appl. Soil Ecol.* **5**, 81–96.

RADEA, C. & ARIANOUTSOU, M. (2000) Cellulose decomposition rates and soil arthropod community in a *Pinus halepensis* Mill. forest of Greece after a wildfire. *Eur. J. Soil Biol.* **36**, 56–64.

SALAMANCA, E.F., RAUBUCH, M. & JOERGENSEN, R.G. (2002) Relationships between soil microbial indices in secondary tropical forest soils. *Appl. Soil Ecol.* **615**, 1–9.

SMOLANDER, A. & KITUNEN, V. (2002) Soil microbial activities and characteristics of dissolved organic C and N in relation to tree species. *Soil Biol. Biochem.* **34**, 651–660.

SOKAL, R.R. & ROHLF, F.J. (1995) *Biometry.* (3rd edn). W. H. Freeman and Company, New York.

The Non-Affiliated Soil Analysis Working Committee. (1990) *Handbook of Standard Soil Testing Methods for Advisory Purposes.* Soil Science Society of South Africa, Pretoria.

WANNER, M. & DUNGER, W. (2002) Primary immigration and succession of soil organisms on reclaimed opencast coal mining areas in eastern Germany. *Eur. J. Soil Biol.* **38**, 137–143.

WARDLE, D.A., NICHOLSON, K.S., BONNER, K.I. & YEATES, G.W. (1999) Effects of agricultural intensification on soil-associated arthropod population dynamics, community structure, diversity and temporal variability over a seven-year period. *Soil Biol. Biochem.* **31**, 1691–1706.

WOOLLEY, T.A. (1982) Mites and other soil micro-arthropods. In: *Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties* (2nd edn). Soil Science Society of America Inc., Madison, Wisconsin, U.S.A., pp. 1131–1142.