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

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; 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; Koehler, 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 series 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 forms 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 x 2 m quadrates were randomly laid out in each site.
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

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

<table>
<thead>
<tr>
<th>Sites</th>
<th>Site age (years)</th>
<th>Substrate characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand 8</td>
<td>1</td>
<td>Sand dune with no horizon differentiation and a thin litter layer derived from annual grasses</td>
</tr>
<tr>
<td>Stand 7</td>
<td>2</td>
<td>Sand dune with no horizon differentiation and a thin litter layer derived mainly from annual indigenous grasses</td>
</tr>
<tr>
<td>Stand 5</td>
<td>10</td>
<td>Sandy soil with a thin organic layer and litter cover from Acacia kosiensis leaves and twigs</td>
</tr>
<tr>
<td>Stand 3</td>
<td>18</td>
<td>Sandy soil with a thin organic layer and a large amount of litter derived from A. kosiensis leaves and dead branches and climbers</td>
</tr>
<tr>
<td>Stand 1</td>
<td>24</td>
<td>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</td>
</tr>
<tr>
<td>Sokhulu</td>
<td>Unknown</td>
<td>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</td>
</tr>
</tbody>
</table>

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
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 paintbrush 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 Bloemfontein, 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 determined 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 extraction 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™ 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 properties. 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, 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 procedure 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 proportion of the total count (or biomass) for the \( i \)th taxa, was used to calculate the Shannon–Wiener diversity index (\( H' \)) using PRIMER™ 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\(^{-2}\), respectively), was more than three times the density of the next most abundant site (the 1-year-old site, with 320 individuals m\(^{-2}\)). The rest of the sites had between 200 and 240 individuals m\(^{-2}\). Families shared between the rehabilitating sites and the benchmark site increased marginally 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
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 Polyspididae 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).
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 & Dufreéne, 1996). This may be ascribed to seasonal differences in the time of sampling as soil micro-arthropod density varies considerably between seasons (Wurdle 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...
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 composition of either the Acari or insects. Potassium (statistically significant), N, P and pH (to some extent, but none significant) partly explained Acari abundance and composition, and none of the soil variables were related to insect composition. Other biotic and abiotic factors must

<table>
<thead>
<tr>
<th>Sites</th>
<th>Age in years</th>
<th>Shannon–Wiener diversity index ($H'$)</th>
<th>Mean number of families or orders</th>
<th>Total number of families or orders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acari</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stand 8</td>
<td>1</td>
<td>0.577 ± 0.2</td>
<td>2.0 ± 0.4&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>6</td>
</tr>
<tr>
<td>Stand 7</td>
<td>2</td>
<td>0.277 ± 0.2</td>
<td>1.2 ± 0.4&lt;sub&gt;b&lt;/sub&gt;</td>
<td>4</td>
</tr>
<tr>
<td>Stand 5</td>
<td>10</td>
<td>0.413 ± 0.2</td>
<td>1.2 ± 0.5&lt;sub&gt;b&lt;/sub&gt;</td>
<td>4</td>
</tr>
<tr>
<td>Stand 3</td>
<td>18</td>
<td>0.438 ± 0.3</td>
<td>1.8 ± 0.5&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>4</td>
</tr>
<tr>
<td>Stand 1</td>
<td>24</td>
<td>0.761 ± 0.2</td>
<td>2.4 ± 0.5&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>5</td>
</tr>
<tr>
<td>Sokhulu</td>
<td>Unknown</td>
<td>1.276 ± 0.4</td>
<td>4.8 ± 1.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>12</td>
</tr>
<tr>
<td>Insects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stand 8</td>
<td>1</td>
<td>0.139 ± 0.1&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>0.6 ± 0.4&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>3</td>
</tr>
<tr>
<td>Stand 7</td>
<td>2</td>
<td>0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.6 ± 0.2&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>3</td>
</tr>
<tr>
<td>Stand 5</td>
<td>10</td>
<td>0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.4 ± 0.2&lt;sub&gt;b&lt;/sub&gt;</td>
<td>2</td>
</tr>
<tr>
<td>Stand 3</td>
<td>18</td>
<td>0.139 ± 0.1&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>0.8 ± 0.4&lt;sub&gt;ab&lt;/sub&gt;</td>
<td>3</td>
</tr>
<tr>
<td>Stand 1</td>
<td>24</td>
<td>0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.4 ± 0.2&lt;sub&gt;b&lt;/sub&gt;</td>
<td>2</td>
</tr>
<tr>
<td>Sokhulu</td>
<td>Unknown</td>
<td>0.561 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2 ± 0.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5</td>
</tr>
</tbody>
</table>
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 similarity 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.

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