J. Zool., Lond. (1996) **238**, 703–712

Millipede communities in rehabilitating coastal dune forests in northern KwaZulu/Natal, South Africa

R. J. VAN AARDE*, S. M. FERREIRA AND J. J. KRITZINGER

Mammal Research Institute, University of Pretoria, Pretoria 0002, RSA

(Accepted 9 December 1994)

(With 1 figure in the text)

The rehabilitation, after mining, of coastal sand dunes north of Richards Bay by Richards Bay Minerals began some 18 years ago, and resulted in the simultaneous availability of a known-aged series of stands representative of coastal dune forest succession.

A survey of the millipede community in this area revealed increases in species diversity and a decrease in their density, with an increase in stand age. Development of these communities is characterized by replacement and addition of species, typical of ecological succession. Colonization of areas disturbed by mining reflects on the species reservoir present in the surrounding unmined forests with apparent pioneer species being either replaced or complemented by the relatively slow invasion of secondary species.

Comparisons of age-specific millipede community variables on rehabilitating dunes with those recorded in relatively undisturbed dunes suggest that the development of communities results from autogenic succession initiated through habitat rehabilitation. With several community parameters in rehabilitating dune forests being similar to those recorded in undisturbed forests, it is concluded that the millipede community can be restored through management options based on principles relating to ecological succession.

Contents

Introduction

Disturbances resulting from drought, floods, fire, and some human activities are considered as mechanisms through which species diversity is maintained (Pickett & White, 1985; Petraitis, Latham & Niesenbaum, 1989). Assessing the response of animal communities to environmental disturbances through describing the actual pattern of changes after disturbance, should lead to

*Address for correspondence

an improved understanding of forces determining community structures, and offer insight into the process of ecological succession (Fox, 1990). However, the determinants of biological diversity may vary with taxonomic groups and environmental conditions (Hendrix, Brown & Dingle, 1988).

The mining of coastal sand dunes north of Richards Bay is preceded by the removal of all surface vegetation and the local disappearance of associated animal life, and can be considered a discrete disturbance event. Post-mining rehabilitation of these dunes by Richards Bay Minerals (RBM) results in ecological succession taking place on these dunes, with the number of plant species increasing over time since the initiation of rehabilitation (Lubke, Moll & Avis, 1992; Mentis & Ellery, 1994). This secondary vegetation succession is expected to be associated, or even be promoted, by a variety of biological interactions, amongst others those affecting nutrient fluxes (Barbour, Burk & Pitts, 1980).

The role millipedes may play in ecosystem nutrient fluxes (see Coleman, Reid & Cole, 1983) suggests that they may be useful indicators of successional changes in community processes. Millipedes are thought to be important in the fragmentation of accumulated leaf litter (Wallwork, 1976), thereby facilitating microbial decomposition as part of soil nutrient cycles (Swift, Heal & Anderson, 1979). Millipede activity apparently accounts for only 10% of total chemical decomposition within a given ecosystem, but their feeding activities may facilitate the role of micro-organisms responsible for about 90% of the total chemical breakdown (Anderson & Bignall, 1980).

Published information on the structure of southern African millipede communities is limited, with the most recent paper being that of Dangerfield & Telford (1992), comparing julid millipedes between habits in the seasonal tropics. Succession following disturbance through mining in Germany has been documented by Dunger & Voigtländer (1992), indicating that the millipede community in 20-year-old woodlands still differed from those in 'natural' woodlands. We know of no other study that investigates the response of millipede communities to perturbations resulting from mining or other forms of habitat disturbance.

This paper reports on successional changes of millipede communities in rehabilitating vegetational stands and relates these to ecological principles. A comparison between millipede communities in rehabilitating stands, a forest disturbed *c.* 30 years ago through forestry activities, and a mature forest is also made.

The study area

The area where dune mining is taking place is situated *c.*15 km north-east of the coastal town Richards Bay (28°43′S, 32°12′E). The study area includes a diverse range of habitat types, these including a series of rehabilitating stands varying in age from a few months to 14 years at the time of the study. The rehabilitating stands are bordered by a seaward belt of unmined coastal dune forest which is fragmented by plantation patches (mainly *Eucalyptus saligna* and *Casuarina equisetifolia*), and on the interior by a narrow strip afforested with *C. equisetifolia* following dune mining. It also includes patches of sand dunes stripped of vegetation in preparation for mining, and dunes being reshaped and prepared for rehabilitation. Inspection of aerial photographs allowed us to age several unmined patches of forest *c.* 30 km north-east of Richards Bay in the Zulti North lease area, ranging from 30 to 50 years in regeneration age at the time of the study.

The method of rehabilitation following mining has been described by Camp (1990). The mechanical reshaping of dunes, followed by the spreading of topsoil collected ahead of mining after forest clearance, results in the development of a series of known-aged stands, varying from young communities dominated by low growing *Acacia karroo* shrublands interspersed with *Dactyloctenium geminatum*, to woodlands also dominated by *A. karroo*, with broad-leaved trees characteristic of the surrounding indigenous forests establishing themselves. Fourteen-year-old rehabilitating areas are characterized by *A. karroo* specimens already beginning to fall over, and by *Sideroxylon inerme*, *Celtis africana*, *Mimusops caffra*, *Vepris undulata*, and *Trichilia emitica* colonizing available space under the *A. karroo* canopy. These species are common in surrounding unmined areas. The ground cover is dominated by *Asystasia gangetica* with the little grass present in older areas mainly represented by *Brachiaria chusqueoides* (Camp, 1990). A management policy of minimum interference is adhered to once rehabilitation has been initiated and currently involves the control of alien invasive plants (Paul Camp, pers. comm.). Millipedes and all vertebrates colonize the area of their own accord.

The vegetation in a patch of forest cleared of vegetation *c*. 30 years ago in the Zulti North lease area is dominated by sparsely distributed *A. karroo*, while similar species, as in 14-year-old rehabilitating areas, form part of the canopy. Vertical structure is much more complex in these areas than in rehabilitating areas. The majority of the vegetation in the Zulti North region consists of mature forest characterized by a large number of woody species. The tree community is dominated by *Trema orientalis* with *Isoglossa* species dominating the shrub layer on the forest floor (Weiser, 1987).

Material and methods

Rehabilitating stands at the time of our survey (December 1992) ranged in age from 0–14 years, with stand 1 representing seral stages 12–14 years old ($\approx$ 83 ha), stand 2 stages 9–11 years old ($\approx$ 139 ha), stand 3 stages 5–8 years old ($\approx$ 55 ha), and stand 4 stages 2–4 years old ($\approx$ 70 ha). In addition, patches of unmined forest which, according to aerial photographs, developed over the last 30 years ($\approx$ 65 ha), and another relatively undisturbed forest in the Zulti North region ($\approx$ 1774 ha) were also used as study locations.

A number of fixed width transects of 35 $\times$ 6 m were randomly located in each of these 6 sites as one-off sampling areas. These were considered easier to sample than square quadrats of equivalent size. The number of transects surveyed in the different stands were as follows: stand 1—18, stand 2—10, stand 3—9, stand 4—14, the 30-year-old forest—10 and Zulti North—3. To account for potential diurnal changes in activity, daily differences in abundance were investigated by grouping all surveys of transects in 4 time periods during the day. These were as follows: Period I–00:00–05:59, Period II—06:00–11:59; Period III—12:00–17:59, and Period IV—18:00–23:59.

Adult millipedes are conspicuously coloured and between 6 and 16 cm in length. All millipedes seen on the ground and on shrubs and trees were collected separately by hand, with the former defined as the 'ground stratum' and the latter as the 'tree stratum' (> 30 cm but < 3 m above ground surface). For practical reasons, millipedes occurring out of reach (> 3 m) could not be collected and identified.

During the study period of 3 weeks, $\approx$ 3200 millipedes were collected and placed into 'species categories'. Specimens of each category were photographed and collected for later identification to species level against reference material at the Natural Science Museum in Durban. One of these categories comprised 2 species and their stand-specific prevalence was recorded during a follow-up survey in October and December 1993. Less than 5% of millipedes collected were juveniles. These could not be identified to species level and were therefore excluded from the analyses.

Density is expressed as the mean number of millipedes/transect for the ground and tree strata. All means are followed by 1 standard error of the mean. Diversity (H) and equitability (E) were calculated as described by Dickman (1968) using the equations $H = -\Sigma(p_i)(\log_2 p_i)$ and $E = H/H_{max}$, where H = index of species diversity, p_i = the proportional abundance of the i'th species, H_{max} = the maximum diversity for the given number of species calculated as $H_{max} = \log_2 S$, where S = number of species. The summation is for all species. Dominance is defined as the proportional contribution of the 2 most common species to total density (Krebs & Wingate, 1976).

Similarities between different stands were calculated using Steinhaus' similarity coefficient, $S = 2W/(A + B)$, where W = sum of the minimum densities of species occurring on the stands being compared, and A and B = total densities of millipedes on these 2 stands (Legendre & Legendre, 1983).

Results

Species composition

Ten 'species' were distinguished by morphological and morphometric characteristics. Eight of these were identified to species level and two to generic level. The communities comprise three different orders, with the order Juliformia represented by seven species, the order Oniscomorpha (pill millipedes) by two species, and the order Polidesmoidea (keeled millipedes) by a single species. One of the 'species' distinguished during the initial surveys on the structure of the community comprised two closely related species (*Centrobolus fulgidus* and *C. richardi*).

The species recorded in the different stands and their numerical abundances are presented in Table I. *Spinotarsus anguliferus* seems to be the first to colonize rehabilitating areas, while *Orthoporus*, *Alloporus*, *Gymnostreptus pontifex*, *Centrobolus sanguinipes*, and *Ulodesmus biconus* were only recorded in unmined areas. Two of these species (*Alloporus* and *C. sanguinipes*) were only recorded in the mature forest. Almost all species found in young stands (3 & 4) also occurred in the older stands, with the exception of a single specimen of *Doratogonus* in stand 4, which was absent from stands 2 and 3 but did occur in the older stands. The number of species recorded in each stand varied from two in stands 4 and 3 to five in stand 1. The 30-year-old unmined area harboured eight species and the mature forest 10 species.

TABLE I

The numerical abundance of 10 millipede 'species' recorded on 6 × 35 m transects on stands of different regeneration ages on the coast of KwaZulu/Natal, South Africa

Species	Zulti North (Mature forest)	Forest (30 years)	Stand 1 (12–14 years)	Stand 2 (9–11 years)	Stand 3 (5–8 years)	Stand 4 (2–4 years)
Doratogonus	23	25	7			1
Centrobolus fulgidus/richardi	65	720	539	1288	434	
Spinotarsus anguliferus	6	11	53	23	83	17
Orthoporus	4	3				
Gymnostreptus pontifex	2	9				
Sphaerotherium rotundatum	10	9	19			
S. dorsale	44	35	4	1		
Ulodesmus biconus	5	11				
Centrobolus sanguinipes	9					
Alloporus	8					
Number of transects sampled	3	10	18	10	9	14
Number of species	10	8	5	3	2	2

TABLE II

Daily activity of millipedes expressed as mean numbers/transect during four time periods in six stands representing rehabilitating areas as well as unmined forest. Values presented as 'means' when only one transect was surveyed represents totals

Habitat type	Variable	Time period 00:00–05:59 I	06:00–11:59 II	12:00–17:59 III	18:00–23:59 IV
Zulti North	Mean		50.33		
(Mature forest)	S.E.		11.39		
	n		3		
Forest	Mean		90.40	68.20	
(30 years old)	S.E.		22.66	11.76	
	n		5	5	
Stand 1	Mean	15.00	75.33	27.50	26.20
(12–14 years old)	S.E.	14.99	16.19	7.58	8.49
	n	2	3	8	5
Stand 2	Mean	57.00	107.50	58.00	166.75
(9–11 years old)	S.E.		47.76		127.88
	n	1	4	1	4
Stand 3	Mean	38.00	92.00	32.00	40.75
(5–8 years old)	S.E.		43.65		15.37
	n	1	3	1	4
Stand 4	Mean	1.00	1.83	0.00	0.50
(2–4 years old)	S.E.	0.58	1.07	0.00	0.50
	n	4	6	2	2

TABLE III

Total number of millipedes recorded at two-hourly intervals on two transects in stand 2 on 16/12/1992

Time of day when counting commenced	Numbers on stratum on Transect A: Ground	Trees	Total	Numbers on stratum on Transect B: Ground	Trees	Total
06:30	393	152	545	38	37	75
08:30	551	80	631	37	29	66
10:30	331	23	354	35	18	53
12:30	290	18	308	31	11	42
14:30	309	23	332	32	7	39
16:30	333	32	365	26	10	36
18:30	279	26	305	19	6	25
CV	24.5%	90.6%	29.4%	20.0%	65.4%	34.0%

Diurnal activity pattern and intra-transect variability

The daily activity of millipedes expressed as mean numbers/transect during four time periods is presented in Table II. Mean numbers/transect differ significantly for stands 1 and 4 ($F_{3,14} = 4.53$, $P < 0.05$; $F_{2,8} = 5.83$, $P < 0.05$ for stands 1 and 4, respectively) but not for stands 2 and 3. The highest densities were recorded during period II in all stands except in stand 2 where the density

TABLE IV

Stratum-specific mean millipede densities in coastal dune forests in KwaZulu/Natal, South Africa. All means are followed by one standard error of the mean and are based on transects conducted during time period II (06:00–11:59). The strata are described in the text

	Stratum	
Stand	Ground	Trees
Zulti North (n = 3)	6.00 ± 1.85	47.00 ± 9.61
Forest (30 yrs) (n = 5)	20.20 ± 9.49	70.20 ± 15.66
Stand 1 (12–14 yrs) (n = 3)	58.67 ± 16.50	16.67 ± 1.45
Stand 2 (9–11 yrs) (n = 4)	103.25 ± 44.74	4.25 ± 3.28
Stand 3 (5–8 yrs) (n = 3)	51.60 ± 40.17	40.33 ± 7.75
Stand 4 (2–4 yrs) (n = 6)	3.67 ± 0.93	0

TABLE V

Mean densities per transect of millipede species occurring during time period II in six coastal dune habitat types in KwaZulu/Natal, South Africa. The means are followed by one standard error of the mean and **n** *= number of transects surveyed during time period II (06:00–11:59 h)*

	Stand					
Species	Zulti North (Mature forest) n = 3	Forest (30 yrs old) n = 5	Stand 1 (12–14 yrs) n = 3	Stand 2 (9–11 yrs) n = 4	Stand 3 (5–8 yrs) n = 3	Stand 4 (2–4 yrs) n = 6
Centrobolus fulgidus/richardi	21.67 ± 7.26	81.20 ± 21.22	71.33 ± 14.24	106.75 ± 47.91	91.00 ± 43.11	
Doratogonus	7.33 ± 1.45	3.40 ± 2.02				0.33 ± 0.26
Spinotarsus anguliferus			3.67 ± 2.03	0.50 ± 0.29	0.33 ± 0.33	3.33 ± 1.04
Orthoporus	1.33 ± 0.88	0.20 ± 0.20				
Gymnostreptus pontifex	0.67 ± 0.33	1.20 ± 0.58				
Sphaerotherium rotundatum	2.00 ± 0.58	0.60 ± 0.40				
S. dorsale	14.33 ± 4.17	3.80 ± 1.86	0.33 ± 0.33			
Ulodesmus biconus						
Centrobolus sanguinipes	2.67 ± 0.66					
Alloporus	3.00 ± 0.58					
Stand-specific mean density	53.33 ± 11.35	90.40 ± 22.66	75.33 ± 16.19	107.50 ± 47.76	92.00 ± 43.65	3.67 ± 0.93

peaked during period IV (166.75 ± 127.88). Subsequent analyses were restricted to time period II, which also allowed comparisons with the 30-year-old forest and the mature forest at Zulti North.

The total number of millipedes recorded at two hourly intervals throughout the day on two transects in stand 2 is presented in Table III. Intra-transect variability based on all the counts obtained during the day is lower for the ground strata (CV = 24.5 & 20.0 for the two transects, respectively) than for the tree strata (CV = 90.6 & 65.4 for the two transects, respectively). These values are lower than those for inter-transect variability (CV = 117.5 & 213.5 for trees and ground, respectively) for the same stand.

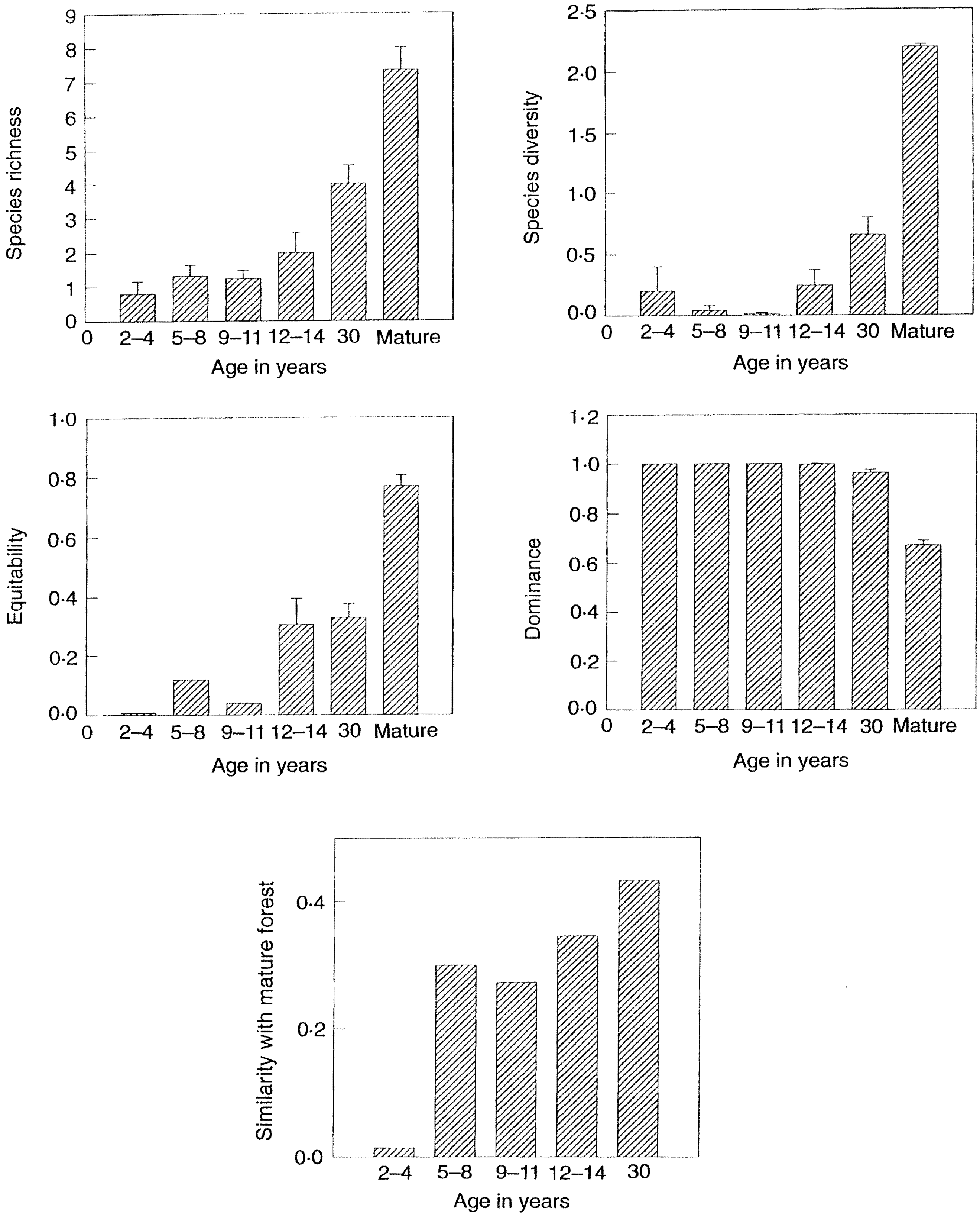

FIG. 1. Mean species richness, diversity, equitability, and dominance of millipedes as a function of habitat age as well as similarity with Zulti North. Error bars represent standard errors of mean values.

Density

Millipede densities for the different strata in the six stands are presented in Table IV. In spite of intra-habitat variability, total densities in the tree stratum are significantly affected by stand age ($F_{4,11} = 7.06$, $P < 0.05$). Densities on the trees peaked in the 30-year-old unmined areas (70.2 ± 15.66 individuals/transect), while the highest density on the ground was recorded in stand 2 (103.25 ± 44.74 individuals/transect). High intra-stand variability in densities of the ground stratum resulted in stand-specific densities not differing significantly ($F_{5,15} = 2.43$, $P > 0.05$). Total density (see Table V), irrespective of stratum for strand 1 (75.33 ± 16.19 individuals/transect), does not differ significantly from that of the unmined 30-year-old forest (90.4 ± 22.66 individuals/transect) ($t_6 = 0.41$, $P > 0.05$).

Species-specific mean densities for all species recorded in more than one stand differ from stand to stand for all species (Table V). The *Centrobolus fulgidus/richardi* category dominated in terms of density in all stands but stand 4, and accounts for the trends in total millipede density across successional stands. However, the mean density for this category in stands 1, 2, 3, and the 30-year-old forest did not differ significantly ($F_{3,11} = 0.187$, $P > 0.05$).

Following the recognition that this category represents two distinct species, an analysis of data collected during December 1993 showed a distinct difference in the habitat preferences of these two species. During this survey, 35.8% ($n = 299$) and 99.8% ($n = 1167$) of the *C. fulgidus/richardi* individuals collected in stand 1 and 2, respectively, were identified as *C. fulgidus*. In the 30-year-old stand and at Zulti North, *C. richardi* comprised 57.0% ($n = 244$) and 91% ($n = 45$) of the category, respectively.

Richness, diversity, equitability, dominance, and similarity

Mean species richness for all strata combined increases with an increase in habitat age (Fig. 1), resulting amongst others from the presence of keeled and pill millipedes, which are absent from the young rehabilitating stands. These trends are also reflected in the estimated mean diversity values which increase with an increase in habitat age (Fig. 1), implying that rehabilitation through succession on mined dunes may result in the development of a community with diversity values similar to those of adjoining unmined areas.

The low indices of diversity in stands 2, 3, and 4 are associated with low equitabilities resulting from the dominance of the *C. fulgidus/richardi* category in stands 2 and 3. Figure 1 illustrates a decrease in dominance only in the unmined areas. Only in the mature forest at Zulti North did all other species combined outnumber the *C. fulgidus/richardi* category. Similarity with Zulti North increases with an increase in regeneration time of mined areas (Fig. 1).

Discussion

The rehabilitating stands represent different stages of coastal dune forest succession, with woody plant species diversity and apparent complexity increasing with stand age (Weiser, 1987; Lubke *et al.*, 1992; Ferreira, 1993; Mentis & Ellery, 1994). The 30-year-old unmined forest is considered as a later stage of coastal dune forest succession (cf. Mentis & Ellery, 1994), while the unmined area at Zulti North represents a 'mature' coastal dune forest of unknown age (cf. Weiser, 1987). For the present investigation these two areas can be considered as 'controls' with which the rehabilitating stands may also be compared.

Succession may be considered as the process of community establishment following severe disturbance, as well as the subsequent development of communities characterized by a continuing non-seasonal and directional local colonization by, and local extinction of, species populations. Succession depends on the availability of species pools from where colonization can take place. In the Richards Bay mining operation, the layout of the mining path results in such refuges being present in the form of a relatively narrow unmined seaward strip along the mining path, as well as fragments of relatively undisturbed forests ahead of, and behind, the mining path. To the landward side, rehabilitating areas are bordered by intensely disturbed areas of plantations and densely inhabited areas. This could still serve as a pool for some species. In addition, topsoil collected prior to mining and spread over bare reshaped dunes as part of the rehabilitation programme could serve as a source through which some species may become established. Colonization of mined areas by millipedes is not assisted through artificial manipulation and thus depends on the abilities of these species to colonize rehabilitating areas on their own.

The trends recorded for the millipede community in rehabilitating stands are in line with those expected in a successional sequence (see Barbour *et al.*, 1980). These trends prevail when one considers the 30-year-old forest as well, even though the 30-year-old forest represents an unmined area disturbed through forestry. In terms of densities, the *C. fulgidus/richardi* category, though not the first to occur on these dunes, follows the trend expected for a pioneer species. In considering relative abundance of these two closely related species in rehabilitating stands of different ages, it follows that the successional development of the millipede community is characterized to some extent by species replacement, with *C. fulgidus* acting as a pioneer and dominating during the early stages (9–11 year old stands), and *C. richardi* dominating during the later stages (12–14 year old stands), as well as in the unmined 30-year-old forest.

It appears as if changes in species composition of the millipede communities consists of simple additions of new species, with the number of species increasing from two in stand 4 (2–4 years old) to five in stand 1 (12–14 years old) to 10 in the mature forest at Zulti North. However, considering species-specific densities, the development of communities is characterized by species replacement during the early stages of development. The trend of a general increase in species numbers while the density of some early colonizing species increases to a peak and then declines, is in agreement with that recorded on reclaimed land in Germany by Dunger & Voigtländer (1992).

The differences between rehabilitating stands and unmined areas is apparent, not only in terms of species-specific densities, species richness, and species diversity, but also in terms of species composition which predominantly results from the absence and/or rarity of some forest specialists (e.g. pill and keeled millipedes) in rehabilitating stands. However, with the oldest rehabilitating stands already having been colonized by at least two species of pill millipedes, typical of unmined areas, it seems as if conditions within the rehabilitating areas are changing to facilitate the establishment of communities with characteristics similar to those of unmined areas. This is supported by the increase in similarity with mature forests at Zulti North as rehabilitating stands increase in age. The increase in species richness and diversity, with an increase in habitat age, implies that rehabilitation through succession could result in the development of a millipede community with characteristics similar to those of unmined areas.

Logistical and financial support have been provided by the University of Pretoria and Richards Bay Minerals and the research conducted under the auspices of the Mammal Research Institute of the University of Pretoria. The interest and support provided by staff of the Tisand Ecology Department and the

Department of Public Relations of RBM is greatly appreciated. Dr Steven Telford assisted in the identification of species and Professor J. D. Skinner commented on the typescript. Field assistance was provided by Lorenz Leumann and Michelle Greyling.

REFERENCES

Anderson, J. M. & Bignell, D. E. (1980). Bacteria in the food, gut content and faeces of the litter-feeding millipede *Glomeris marginata* (Villers). *Soil Biol. Biochem.* **12:** 251–254.

Barbour, M. G., Burk, J. H. & Pitts, W. D. (1980). *Terrestrial plant ecology.* Menlo Park, California: Benjamin/Cummings.

Camp, P. D. (1990). Rehabilitation after dune mining at Richards Bay Minerals. *SA Mining World.* October 1990.

Coleman, D. C., Reid, C. P. P. & Cole, C. V. (1983). Biological strategies of nutrient cycling in soil systems. *Adv. Ecol. Res.* **13:** 1–54.

Dangerfield, J. M. & Telford, S. R. (1992). Species diversity of Julid millipedes: between habitat comparisons within the seasonal tropics. *Pedobiologia* **6:** 321–329.

Dickman, M. (1968). Some indices of diversity. *Ecology* **49:** 1191–1193.

Dunger, W. & Voigtländer, K. (1992). Succession of Myriapoda in primary colonization of reclaimed land. In *Proceedings of the 7th International Congress of Myriapoda.* Minelli, A. (Ed.). Leiden: E. J. Brill.

Ferreira, S. M. (1993). *The effect(s) of habitat rehabilitation at Richard's Bay on small mammal community structure.* MSc thesis, University of Pretoria.

Fox, B. J. (1990). Changes in the structure of mammal communities over successional time scales. *Oikos* **59:** 321–329.

Hendrix, S. D., Brown, V. K. & Dingle, H. (1988). Arthropod guild structure during old field succession in a new and old world site. *J. Anim. Ecol.* **57:** 1053–1066.

Krebs, C. J. & Wingate, I. (1976). Small mammal communities of the Kluane Region, Yukon Territory. *Can. Fld-Nat.* **90:** 379–389.

Legendre, L. & Legendre, P. (1983). *Numerical ecology.* Amsterdam: Elsevier Scientific Publishing Co.

Lubke, R. A., Moll, J. B. & Avis, A. M. (1992). Rehabilitation ecology. *Coastal & Environmental Services, Environmental Impact Assessment. Eastern Shores of Lake St Lucia (KINGSA/TOJAN Lease area)*: 251–303.

Mentis, M. T. & Ellery, W. N. (1994). Post-mining rehabilitation of dunes on the north-east coast of South Africa. *S. Afr. J. Sci.* **90:** 69–74.

Petraitis, P. S., Latham, R. E. & Niesenbaum, R. A. (1989). The maintenance of species diversity by disturbance. *Q. Rev. Biol.* **64:** 393–418.

Pickett, S. T. A. & White, P. S. (Eds) (1985). *The ecology of natural disturbance and patch dynamics.* Orlando: Academic Press.

Swift, M. J., Heal, O. W. & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems.* Oxford: Blackwell.

Wallwork, J. A. (1976). *The distribution and diversity of soil fauna.* London: Academic Press.

Weiser, P. J. (1987). Dune vegetation between Richards Bay and Mfolozi River Mouth based on a vegetation survey. *Natal Town and Regional Planning Report* **38.** Pietermaritzburg.