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The influence of millipedes on selected soil elements: a microcosm study on three species occurring on coastal sand dunes

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Summary

1. The effect of mechanical breakdown of detritus by the millipedes *Centrobolus fulgidus*, *Centrobolus richardii* and *Spinotarsus* sp. on selected soil elements was investigated in the laboratory.

2. Microcosms containing soils, detritus and millipedes from areas undergoing vegetation regeneration were set up in a climate chamber. Short-term changes in soil concentrations of ammonia (NH^{4+}), nitrates (NO^{3-}), phosphorus (P), calcium (Ca), potassium (K), magnesium (Mg), nitrogen (N) and carbon (C) in the presence and absence of millipedes were determined.

3. Soil concentrations of the elements investigated were higher in microcosms subjected to millipede activity than in controls. Microcosms containing *Spinotarsus* sp. and *C. richardii* were found to have the highest concentrations of Mg, K, N and C.

4. The results further illustrated no major sex-specific differences for individual species.

5. For most elements, rates of change were not affected by millipede biomass. However, the largest effect was in rate of change of Mg and K measured at 5–15 g of millipedes per microcosm.

6. Compositional effects (species present) were recorded for rates of change in K concentrations.

7. Influence of species richness on rates of change was only recorded for K and N, with rates for both increasing as the number of species increased. The predictability of rate of change diminished for K with an increase in the number of species.

8. It is concluded that millipedes influence concentrations of soil elements through species-specific differential effects. Patterns related to composition and species richness only reflect species-specific differences. Nevertheless, the rate at which these soil elements increase in the microcosms suggests that millipede activity may accelerate the release of elements in areas undergoing vegetation development on coastal dune forests.

Key-words: Microcosms, millipedes, species composition, species richness

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Introduction

Millipedes as detritivores apparently affect nutrient cycling through the redistribution of organic material and, consequently, the release of chemical elements such as nitrogen in the soil (Dangerfield & Milner 1996). Since nutrient cycling is one of the key processes governing ecosystem dynamics (Tilman, Wedin & Knops 1996), millipedes may have profound influences on ecosystems. Generally, millipedes are responsible for ingesting 5–10% of the annual leaf litter fall of temperate systems (Van der Drift 1975) but their impact may vary depending on the species.

The millipede communities in the regenerating coastal dune forests at Richards Bay, South Africa, comprise at least 13 species (van Aarde, Ferreira & Kritzinger 1996a). Of these, at least two species, *Centrobolus fulgidus* (Lawrence 1967) and a *Spinotarsus* species (Museum of KwaZulu-Natal, Durban, specimen NM 15855), dominate either in the soil or on the soil surface with a third species, *Centrobolus richardii* (Lawrence 1967), also inhabiting the forest shrub substratum, but feeding on detritus.

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Recent studies by van Aarde, Smit & Claassens (1998) showed directional changes in selected soil elements with regeneration age of postmining rehabilitating areas. This raises the possibility that organisms living in or on the soil may affect changes in these elements. Since the activities of *C. fulgidus* and *Spinotarsus* sp. are restricted to the soil and soil surface, inevitably their activities may affect the rate of change of these elements in the soil which could indicate what impact millipedes may have in this rehabilitating ecosystem. However, since *C. richardii* also feeds on detritus, the impact of this species also needs to be considered. It is therefore conceivable that these three species will be of interest in determining whether or not millipede activity influences changes in soil elements over time and at what rate this occurs.

The present study consisted of three phases. During the first phase we investigated whether the presence of millipedes brings about changes in soil element concentrations. We had to consider the possibility that different abundance or biomass of millipedes is likely to affect the rate of element release determining the concentrations of elements in the soil. Thus, in the second phase the relationship between species-specific abundance (biomass) and rate of soil element release in the soil was investigated. As part of the second phase, sex-specific variation was also quantified.

Since the number and/or type of millipede species may also affect soil elements, the third phase considered the influence of millipede species richness and composition on rates of element release in the soil. As part of the study, four hypotheses concerning the importance of number of species for ecosystem functioning stated by Lawton (1994) were considered. The first possibility is no response to changing number of species as it is unimportant how many millipede species constitute a community – the null hypothesis (Lawton 1994). Another possibility is that a change in species richness may affect the rate of element release with the outcome of change being unpredictable – the idiosyncratic hypothesis.

The corollary to the idiosyncratic hypothesis is that the addition or removal of millipede species could have an effect on the rate of element change as long as there are less than say 10 species present, but that subsequent additions or removals may have no effect. This suggests that a specific minimum number of millipede species may be needed to maintain an optimal rate of element release but, thereafter, additional species will show no marked changes in the rate at which this occurs (the redundancy hypothesis) (Walker 1992; Lawton & Brown 1993). In contrast, the rivet hypothesis (Ehrlich & Erhlich 1981) states that all species contribute to the functional processes of an ecosystem and that removal of any one of them will impair these processes. These hypotheses are considered as a background to testing the relationship between species richness (number of species) and the rate of change in soil element concentrations, and directed the formulation of the following hypotheses to be tested in the present investigation:

1. The presence of millipedes affects the rate at which elements accumulate in the soil.
2. Biomass of a single millipede species influences the rate at which elements accumulate in the soil.
3. Sexes of a single millipede species influence the rate at which elements accumulate in the soil differentially.
4. Individual millipede species affect the rate at which elements accumulate in the soil differentially.
5. A change in millipede species richness affects the rate at which elements accumulate in the soil.

Materials and methods

STUDY ANIMALS

Millipedes were collected in areas undergoing vegetation regeneration near Richards Bay where they were found to occur in highest abundance. They were maintained in glass tanks (30 cm × 15 cm × 15 cm) containing soil and detritus collected from these same areas. Additional detritus to be used during the experiment was collected in these same areas and dried in a ventilation oven at 65 °C. Topsoil spread over dunes prior to the initiation of the rehabilitating process was also collected and dried at the same temperature and both the detritus and soil were kept in a laboratory at 25·5 °C until used.

PHASE I: THE INFLUENCE OF THREE MILLIPEDE SPECIES ON SOIL ELEMENT CONCENTRATIONS (FEBRUARY–MARCH 1997)

Two-litre plastic containers (10 control and 10 treatment replicates) with a 12-cm × 12-cm base and screw-on lid were used as microcosms. Topsoil (dry mass ≈250 g) was added to each microcosm and a representative subsample taken per microcosm and analysed for mineral content.

Detritus (dry mass ≈50 g) was weighed separately and added to the microcosm before the addition of male *C. fulgidus* millipedes ($n = 10$ individuals) weighing ≈10 g in total per microcosm. Controls were set up in the same way but contained no millipedes. The microcosms were moistened daily by spraying ≈5 ml of distilled water from a fine nozzle spray-gun bottle to prevent dehydration. The trial was allowed to continue for 18 days (until most of the detritus appeared broken down). Subsequently, millipedes were again weighed and soil subsamples obtained as before for post-treatment analysis.

For *C. richardii* and *Spinotarsus* sp., trials were set up in the same way, excepting that 10 microcosms containing *Spinotarsus* sp. ($n = 10$ individuals) weighing

≈5 g and 10 microcosms containing *C. richardii* (n = 10 individuals) weighing ≈13 g were used together with 10 controls (0 g). These trials were run for 25 days (until most of the detritus appeared broken down). All trials were conducted in a humidity chamber at 60% relative humidity with temperature 25 °C and a 12-h dark, 12-h light cycle.

PHASE II: THE INFLUENCE OF BIOMASS AND SEX OF THREE MILLIPEDE SPECIES ON SOIL ELEMENT CONCENTRATIONS (OCTOBER 1997)

Microcosms were set up in a humidity chamber at 60% relative humidity and a temperature of 25 °C. Each microcosm contained the following: ≈250 g dry mass sand, ≈50 g dry mass detritus and a specified biomass of millipedes (with exception of the controls with no millipedes). Microcosms containing biomasses of 5 g, 15 g and 25 g (restricted by the availability of individuals) of either males or females of a given species, were set up in the laboratory together with controls containing no millipedes. The trial was run for 18 days (until most of the detritus appeared broken down). Random subsamples of the soil were taken per microcosm prior to exposing it to millipedes and postexposure to millipedes and analysed for P, Mg, K, N and C content (the elements found to be most affected by millipede activities during Phase I).

PHASE III: MILLIPEDE SPECIES RICHNESS AND COMPOSITION INFLUENCES ON SOIL ELEMENT CONCENTRATIONS (NOVEMBER 1997)

Microcosms were set up as before with treatments divided into four groups. In the first instance five microcosms were set up as controls with no millipedes. In the second instance 15 microcosms each containing ≈12 g of one of the three species of millipedes (n = 5 per species) were set up. The third group comprised 15 microcosms each containing ≈12 g per two-species combination (≈6 g per species) per microcosm. The three species used resulted in three possible combinations of two species (n = 5 microcosms per two-species combination). The final group comprised five microcosms containing ≈12 g of one combination of all three species (≈4 g per species per microcosm). At the start of each trial soil subsamples were collected as for Phase I prior to millipedes being added to the microcosms. The trial was run for 18 days (until most of the detritus appeared broken down) after which soil subsamples were collected again. Soil subsamples were analysed for P, Mg, K, N and C content.

CHEMICAL ANALYSES

Five subsamples from the upper 2 cm of soil in each microcosm were mixed and a representative aliquot of soil (≈50 g) per microcosm analysed. The determination of NH^{4+}, NO^{3-}, P, Ca, Mg, K, N and C concentrations followed the procedures suggested by the Non-affiliated Soil Analysis Working Committee (1990). Nitrogen was determined by the Kjeldahl method of digestion by sulphuric acid and organic carbon by the Walkley–Black method. Phosphorus was determined using the Bray-I method and determined caolorimetrically by the molybdeinum blue method. Calcium and Mg concentrations were determined by atomic absorption spectroscopy whereas K was determined by flame emission spectroscopy.

STATISTICAL ANALYSES

For Phase I, means and standard errors were calculated for all elements analysed both pre- and post-treatment and a two-way ANOVA with replication (Sokal & Rohlf 1981) conducted to investigate the influence of the presence of *C. fulgidus, C. richardii* and *Spinotarsus* sp. on NH^{4+}, NO^{3-}, P, Ca, K, Mg, N and C concentrations (mg kg^{-1}) in the soil substrate. Additionally, means and standard errors of the rate of change from pre-to post-treatment in NH^{4+}, NO^{3-}, P, Ca, K, Mg, N and C concentrations per gram millipede per day were calculated on completion of the experiment. A one-way ANOVA was conducted to investigate whether the three species individually had different effects on the rate of change of concentrations of these soil elements. Tukey multiple range tests (Sokal & Rohlf 1981) were used to elucidate differences between millipede species in their influence on NH^{4+}, NO^{3-}, P, Ca, K, Mg, N and C concentrations.

For Phase II, means and standard errors were calculated for the rate of change from pre- to post-treatment in P, K, Mg, N and C. Student's t-tests assuming unequal variance (Sokal & Rohlf 1981) were conducted to investigate whether millipede sexes influence rate of change of soil element concentrations differently. Means and standard errors were also calculated for rate of change from pre- to post-treatment in P, K, Mg, N and C for biomass of 5 g, 15 g and 25 g irrespective of sex, and Kruskal–Wallis ANOVA (Sokal & Rohlf 1981) used to determine at which biomass rates of change in P, K, Mg, N and C were most affected.

For Phase III, means and standard errors were calculated for the rate of change from pre- to post-treatment in P, K, Mg, N and C for every combination of species. To elucidate compositional effects, one-species and two-species microcosms were used in two separate analyses. For each analysis, differences in the rate of change in P, K, Mg, N and C between microcosms comprising different species compositions were investigated using Kruskal–Wallis ANOVA (Sokal & Rohlf 1981). Rates of change irrespective of species composition were compared using

Kruskal–Wallis ANOVA (Sokal & Rohlf 1981). Finally, Bartlett's χ-square test (Sokal & Rohlf 1981) was used to compare variation in rates of change in P, K, Mg, N and C between microcosms comprising zero, one, two or three species.

Results

PHASE I

Concentrations of P, Ca, Mg, K, N and C in the *C. fulgidus* trial were greater for post-treated soils than pretreated soils irrespective of treatment (control or experiment). However, concentrations of Mg, K, N and C were also greater for soils subjected to *C. fulgidus* activity than for the concentrations of these same elements in soils of controls (Table 1). Concentrations of NH^{4+}, P, Mg, K, N and C for soils subjected to activity of *Spinotarsus* sp. and *C. richardii* were greater for post-treated soils than pretreated soils irrespective of treatment. Concentrations of NH^{4+}, Mg, K, N and C were higher for soils subjected to *C. richardii* and *Spinotarsus* sp. activity than for soils with no millipede activity. Concentrations of Ca were also higher for soils subjected to *C. richardii* compared with soils with no millipede activity (Table 1).

The rates of change in concentrations of NH^{4+}, P, K, Mg, N and C per gram millipede per day were greater for *Spinotarsus* sp. and *C. richardii* than for *C. fulgidus*. For all these elements however, the mean rates of change of all elements in soils subjected to *C. Richardii* activity were the greatest (Table 2).

For ease of measurement and as a result of the change in concentrations recorded for P, Mg, K, N and C in Phase I, only these elements were used for further investigations.

PHASE II

Rates of change in concentrations of three soil elements (P, N and C) were not influenced by millipede biomass irrespective of sex. No sex-specific differences were recorded for any of the elements with the exception of Mg. For both Mg and K the highest rates of change in soil concentrations were recorded for soils exposed to 5–15 g biomass of *C. fulgidus* and *Spinotarsus* sp., with no biomass influence recorded for soils exposed to *C. richardii* (Table 3).

Table 1. The influence of the presence of *Centrobolus fulgidus, C. richardii* and *Spinotarsus* sp. on selected soil chemical variables. Chemical variables are presented as mean (±SE) concentrations mg kg^{-1}. 'A' represents results of *F*-test comparing pre- and post-treatments, 'B' represents results of *F*-test comparing control and experiment. 'A × B' represents an interaction

	Control		Experiment		$F_{(1,36)}$-value		
	Pre	Post	Pre	Post	A	B	A × B
Centrobolus fulgidus							
NH_4^+	0·40 ± 0·52	1·10 ± 0·32	0·60 ± 0·58	1·00 ± 0·67	3·67	0·03	0·27
NO_3^-	9·50 ± 8·26	2·00 ± 1·70	6·10 ± 5·95	5·90 ± 8·70	3·41	0·03	3·08
P	4·31 ± 0·18	6·72 ± 1·76	4·52 ± 0·42	7·01 ± 1·61	40·60*	0·43	0·01
Ca	2·25 ± 0·10	2·45 ± 0·15	2·27 ± 0·06	2·37 ± 0·07	21·74*	0·81	2·51
Mg	53·10 ± 2·02	80·80 ± 8·20	53·50 ± 1·18	87·80 ± 6·34	340·31*	4·85*	3·86
K	12·45 ± 1·25	34·60 ± 9·98	12·32 ± 0·78	49·00 ± 7·39	221·22*	13·02*	13·49*
N	61·90 ± 59·14	217·00 ± 104·27	61·40 ± 65·63	350·20 ± 117·58	60·62*	5·42*	5·50*
C	0·05 ± 0·03	0·54 ± 0·16	0·06 ± 0·03	0·72 ± 0·23	161·23*	4·81*	3·97
Centrobolus richardii†							
NH_4^+	0·00	0·80 ± 0·63	0·00	3·00 ± 1·33	35·84*	8·26*	1·30
NO_3^-	2·40 ± 0·52	2·40 ± 4·95	2·30 ± 1·34	5·90 ± 4·56	5·20*	0·51	1·04
P	3·59 ± 0·11	11·57 ± 3·43	3·11 ± 0·21	16·11 ± 5·32	48·37*	2·12	0·36
Ca	2·10 ± 0·05	2·17 ± 0·08	2·17 ± 0·12	2·38 ± 0·26	5·37*	8·37*	1·09
Mg	55·10 ± 1·45	104·3 ± 21·93	57·00 ± 1·33	164·90 ± 61·60	30·92*	5·81*	1·22
K	8·60 ± 0·97	45·90 ± 12·45	12·20 ± 1·14	92·20 ± 22·94	68·59*	10·24*	1·29
N	43·00 ± 62·04	483·80 ± 263·06	67·10 ± 68·26	1209·80 ± 588·56	28·76*	6·30*	1·22
C	0·02 ± 0·01	1·24 ± 0·26	0·04 ± 0·02	2·34 ± 0·93	50·41*	8·27*	1·29
Spinotarsus sp.†							
NH_4^+	0·00	0·80 ± 0·63	0·00	2·40 ± 1·65	23·13*	5·26*	1·21
NO_3^-	2·40 ± 0·52	2·40 ± 4·95	1·80 ± 0·79	6·00 ± 1·83	7·40*	2·21	0·95
P	3·59 ± 0·11	11·57 ± 3·43	3·53 ± 0·20	12·46 ± 3·15	54·54*	0·03	1·06
Ca	2·10 ± 0·05	2·17 ± 0·08	1·93 ± 0·60	2·42 ± 0·16	1·10	4·14*	0·95
Mg	55·10 ± 1·45	104·3 ± 21·93	56·30 ± 1·34	190·20 ± 55·33	42·08*	9·01*	1·31
K	8·60 ± 0·97	45·90 ± 12·45	8·90 ± 0·88	86·20 ± 13·01	110·72*	5·55*	1·22
N	43·00 ± 62·04	483·80 ± 263·06	22·00 ± 3·59	1024·70 ± 412·00	39·32*	2·76	1·22
C	0·02 ± 0·01	1·24 ± 0·26	0·05 ± 0·03	2·27 ± 0·75	63·61*	9·04*	1·29

*Significant test statistics at the 95% level are indicated by *.
†*C. richardii* and *Spinotarsus* sp. investigated simultaneously resulting in the same control for both (see Materials and methods).

Table 2. Comparison of effects of three millipede species on soil chemical variables (mean Δmg kg^{-1} g-millipede^{-1} day^{-1} ± SE). The results of one-way ANOVA are presented with means associated with the same letter in a row not significantly different from each other (Tukey multiple range test)

	C. fulgidus (n = 10)	*C. richardii* (n = 10)	*Spinotarsus* sp. (n = 10)	$F_{(2,27)}$-value	P-value
NH_4^+	0·002 ± 0·003^b	0·016 ± 0·003^a	0·013 ± 0·002^a	6·74	<0·01
NO_3^-	2·9E^{-4} ± 0·018	0·296 ± 0·005	0·015 ± 0·006	1·71	0·20
P	0·012 ± 0·002^b	0·063 ± 0·007^a	0·055 ± 0·007^a	22·56	<0·01
Ca	0·458 ± 0·155^a	3·467 ± 1·511^b	0·870 ± 0·224^a	3·39	0·05
Mg	0·160 ± 0·010^a	0·936 ± 0·111^b	0·455 ± 0·081^c	24·30	<0·01
K	0·171 ± 0·011^a	0·549 ± 0·032^b	0·338 ± 0·030^c	52·93	<0·01
N	1·352 ± 0·216^b	6·929 ± 0·850^a	4·800 ± 0·794^a	17·00	<0·01
C	0·003 ± 0·000^a	0·016 ± 0·002^b	0·009 ± 0·001^c	31·00	<0·01

Table 3. The effects of biomass of three species of millipedes on selected soil chemical variables. Data are presented as mean Δmg kg^{-1} (± SE) over 18 days. The results of Kruskal–Wallis tests are presented with means associated with the same letter in a row not significantly different from each other (Mann–Whitney U-tests)

	Control (n = 3)	5 g	15 g	25 g	H-value	P-value
*Centrobolus fulgidus**						
P	3·48 ± 1·67	5·53 ± 2·00	6·08 ± 2·75	4·97 ± 1·00	$H_{3,N=20}$ = 2·57	0·46
Mg	6·67 ± 21·55^a	66·00 ± 34·21^b	57·17 ± 40·47^b	21·29 ± 33·13^a	$H_{3,N=20}$ = 8·66	0·03
K	12·67 ± 10·97^a	57·25 ± 27·28^b	53·50 ± 23·58^b	1·43 ± 91·39^a	$H_{3,N=20}$ = 7·82	0·05
N	370·67 ± 132·76	566·50 ± 203·11	576·50 ± 110·63	548·86 ± 137·89	$H_{3,N=20}$ = 3·66	0·30
C	2·73 ± 1·05	7·85 ± 4·04	6·85 ± 3·20	6·34 ± 2·87	$H_{3,N=20}$ = 6·02	0·11
Centrobolus richardii†						
P	3·48 ± 1·67	3·43 ± 0·86	4·16 ± 0·47	4·46 ± 0·43	$H_{3,N=13}$ = 2·76	0·43
Mg	6·67 ± 21·55	35·75 ± 31·63	28·67 ± 46·50	61·00 ± 32·08	$H_{3,N=13}$ = 5·84	0·12
K	12·67 ± 10·97	32·25 ± 21·09	47·33 ± 32·50	56·33 ± 24·95	$H_{3,N=13}$ = 5·14	0·16
N	370·67 ± 132·76	557·25 ± 213·83	423·00 ± 409·00	458·33 ± 374·28	$H_{3,N=13}$ = 1·56	0·67
C	2·73 ± 1·05	4·00 ± 2·01	2·93 ± 4·04	4·13 ± 5·68	$H_{3,N=13}$ = 4·08	0·25
Spinotarsus sp.‡						
P	3·48 ± 1·67	3·70 ± 0·98	6·80 ± 1·81	5·27 ± 1·57	$H_{3,N=11}$ = 5·45	0·11
Mg	6·67 ± 21·55^c	78·33 ± 41·96^{ab}	104·00 ± 14·80^a	34·00 ± 7·07^{bc}	$H_{3,N=11}$ = 7·93	0·05
K	12·67 ± 10·97^b	63·00 ± 24·64^{ab}	93·00 ± 26·15^a	45·00 ± 12·73^{ab}	$H_{3,N=11}$ = 8·06	0·04
N	370·67 ± 132·76	510·33 ± 160·94	711·67 ± 220·36	771·40 ± 160·37	$H_{3,N=11}$ = 6·42	0·09
C	2·73 ± 1·05	5·37 ± 3·44	8·90 ± 3·22	10·45 ± 6·29	$H_{3,N=11}$ = 6·91	0·07

*5 g, n = 4; 15 g, n = 6; 25 g, n = 7.
†5 g, n = 4; 15 g, n = 3; 25 g, n = 3.
‡5 g, n = 3; 15 g, n = 3; 25 g, n = 2.

PHASE III

For microcosms comprising only one species, significantly higher rates of change in K concentrations of soil exposed to *Spinotarsus* sp. were recorded compared with soils not exposed to any millipede species. For microcosms comprising two species, significantly higher rates of change in K concentrations of soil exposed to combinations containing *Spinotarsus* sp. and *C. fulgidus* were recorded compared to soils exposed to no species. No differences in rates of change in concentrations relating to species composition were recorded for the other elements or species combination (Table 4).

Rates of change in concentrations of P, Mg and C were not influenced by the number of species (P: $H_{3,N=40}$ = 2·72, P = 0·44; Mg: $H_{3,N=40}$ = 1·62, P = 0·66; C: $H_{3,N=40}$ = 3·22, P = 0·56) to which soils in microcosms were exposed, disregarding species composition. However, rates of change in K concentrations increased in the presence of millipedes ($H_{3,N=40}$ = 13·38, P = 0·01). Note that one, two or three species had similar effects (Fig. 1).

Rates of change in N concentration also increased with an increase in number of species ($H_{3,N=40}$ = 8·81, P = 0·02), but in this case two and three species had a higher effect than none or one species (Fig. 1). Note that for P, Mg and C no variation in rates of change was related to the number of species (P: χ^2_3 = 4·04, P = 0·26; Mg: χ^2_3 = 0·76, P = 0·86; C: χ^2_3 = 4·15, P = 0·24). Variation in rates of change in K concentrations increased with richness (χ^2_3 = 10·05, P = 0·02), while that of N peaked at two species (χ^2_3 = 20·54, P = 0·01).

Table 4. Compositional effects of artificially constructed millipede communities comprising one, two and three species, respectively. Data are presented as mean Δmg kg^{-1} ($\pm$ SE) over 18 days. The results of Kruskal–Wallis tests are presented with means associated with the same letter in a row not significantly different from each other (Mann–Whitney *U*-tests). Sample size equals 5 for all means

One species

	Control	*C. fulgidus*	*C. richardii*	*Spinotarsus* sp.	*H*-value	*P*-value
P	2·61 ± 1·42	3·15 ± 89	2·52 ± 1·89	2·71 ± 1·84	$H_{3,N=20}$ = 1·15	0·77
Mg	23·98 ± 4·75	24·50 ± 4·43	24·83 ± 1·40	28·00 ± 8·32	$H_{3,N=20}$ = 0·69	0·88
K	27·52 ± 1·64^{a}	38·32 ± 5·33^{ab}	38·15 ± 4·16^{ab}	42·34 ± 9·23^{b}	$H_{3,N=20}$ = 11·21	0·01
N	118·72 ± 13·04	122·08 ± 17·85	120·87 ± 12·54	122·64 ± 10·87	$H_{3,N=20}$ = 0·21	0·98
C	0·72 ± 0·51	2·06 ± 0·43	1·10 ± 0·97	1·66 ± 0·83	$H_{3,N=20}$ = 7·81	0·06

Two species

	Control	*C. fulgidus* *C. richardii*	*C. fulgidus* *Spinotarsus* sp.	*C. richardii* *Spinotarsus* sp.	*H*-value	*P*-value
P	2·61 ± 1·42	3·43 ± 0·84	2·73 ± 0·93	3·21 ± 0·59	$H_{3,N=20}$ = 2·10	0·55
Mg	23·98 ± 4·75	23·50 ± 5·47	25·88 ± 4·89	23·34 ± 2·13	$H_{3,N=20}$ = 1·04	0·79
K	27·52 ± 1·64^{a}	39·46 ± 4·37^{ab}	42·40 ± 5·79^{b}	37·22 ± 3·03^{ab}	$H_{3,N=20}$ = 8·80	0·03
N	118·72 ± 13·04	138·32 ± 49·69	148·40 ± 22·90	172·20 ± 61·29	$H_{3,N=20}$ = 5·54	0·14
C	0·72 ± 0·51	1·36 ± 1·44	1·86 ± 1·44	1·60 ± 1·00	$H_{3,N=20}$ = 2·57	0·47

Three species

	Control	*C. fulgidus* *C. richardii* *Spinotarsus* sp.	*Z*-value	*P*-value
P	2·61 ± 1·42	2·45 ± 0·83	–0·31	0·75
Mg	23·98 ± 4·75	23·16 ± 5·32	–0·31	0·75
K	27·52 ± 1·64^{a}	43·02 ± 9·68^{b}	–2·61	0·01
N	118·72 ± 13·04	154·00 ± 31·77	–1·78	0·08
C	0·72 ± 0·51	1·00 ± 1·25	–0·10	0·92

Discussion

Rehabilitating coastal dunes undergoing floral and faunal development north of Richards Bay have thus far been distinguished by changes in structural criteria such as the physical composition or arrangements of plant and animal communities (van Aarde *et al.* 1996b) or soil characteristics (van Aarde *et al.* 1998), rather than process-oriented criteria such as decomposition rates or nutrient cycling. Living entities generally, but more specifically within these coastal dunes, may variously affect process-oriented criteria by for instance, increasing or decreasing the rate of a process (Martinez 1996). This suggests that the functional role of living entities may differ. For instance, although millipedes can utilize 12% of the primary production of certain favourable habitats (Dangerfield & Milner 1996), their impact on decomposition processes and consequently soil element concentrations may vary depending on the species. Also, soil animals such as millipedes can have both a direct effect on soil nutrients by producing faeces and urine which change the quality of the soil substrate, or an indirect effect through eating microorganisms and detritus.

In this respect, the high densities of millipedes in developing forests at Richards Bay (van Aarde *et al.* 1996a) suggest that there may be an indirect impact on the soil substrate through the fragmentation of detritus and subsequent release of elements into the soil. The quantitative differences between the effects of three millipede species (*C. fulgidus*, *Spinotarsus* sp. and *C. richardii*) on element concentrations recorded in the present study, suggest that the functional role of each may differ. This is particularly relevant when considering that all three species do affect the concentration of elements in the soil substrate in the microcosms as compared with the controls. *Spinotarsus* sp. activity contributed to a higher concentration of Mg than the other two species and *C. richardii* activity contributed to a higher concentration of K and most other elements. However, *C. richardii* activity resulted in a faster rate of accumulation of soil elements than the other two millipede species. This is not surprising when considering the distribution of *C. richardii* which is found both in the detritus layer and the top 2 cm of the soil substrate (A.-M. Smit and R. J. van Aarde, personal observation) and possibly also the activity pattern of this species as compared with the other two (Greyling, van Aarde

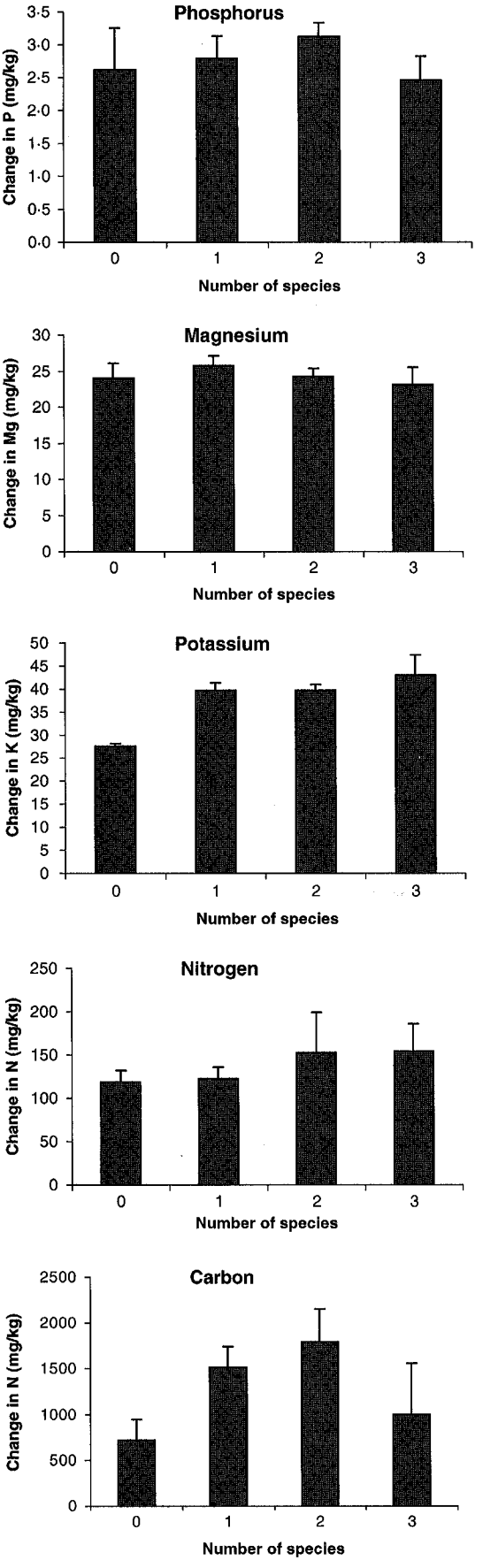

Fig. 1. The influence of millipede species richness on rates of change in soil element concentrations for P, Mg, K, N and C (Mean ±SE).

& Ferreira 2000). Nevertheless, our results do not refute our first hypothesis and rather illustrate that the presence of millipedes does affect the rate at which elements accumulate in the soil.

Our results infer that these species belong to the same functional group within the ecosystem. The differences between their quantitative effects on soil elements particularly during Phase I, however, suggest that their role within this functional group may differ, supporting our fourth hypothesis: individual millipede species affect the rate at which elements accumulate in the soil differently. This may be particularly important when considering the occurrence of the different millipede species at different stages in the successional process at Richards Bay. For example, van Aarde *et al.* (1996b) described mass tree mortality resulting in high detritus biomass on stands dominated by *Spinotarsus* sp. The rate at which individuals of this species mobilize elements may be particularly important in these stands with high detritus biomass. This element mobilization into the soil may have profound influences on later stages of plant succession.

It is furthermore important to distinguish between the quantitative effects due to either direct or indirect millipede activity. Indirect effects can be masked by the direct effects of element release from faeces in the soil substrate, whereas direct effects could be masked by element mobilization as a result of stimulated microbial activity. That microbial activity is an important factor is clear from results obtained from the controls. Microcosms subjected to millipede activity had generally significantly higher concentrations of most elements than the controls. However, the increased concentrations of NH^{4+}, NO^{3-} and especially N postexperimentally, compared with the pre-experimental values for controls, suggest that the role of nitrifying bacteria (which convert NH^{4+} to nitrate), nitrogen-fixing bacteria (which reduce N to NH^{4+} for assimilation) and denitrifying bacteria (which form N from nitrate and nitrite) naturally present in the detritus, should not be excluded. In some instances, elements already present in the detritus as a result of microbial activity prior to detritus being added to the microcosm, may simply have leached into the soil. However, the non-significant increases in concentrations of NH^{4+} and NO^{3-} in the presence of millipedes could be a result of the continued release and utilization of these elements so that differences may not necessarily be detected over the short term. In contrast, the significantly higher concentrations of N in all soils subjected to millipede activity over the short term suggests that millipedes may play an important role in the mobilization of N, especially considering that N is a limiting element in most ecosystems (Symstad *et al.* 1998).

The significant increase in K concentrations for all soils subjected to millipede activity could be related to the high content of K in the millipede faeces since

the presence of animal faeces increases the availability of K (Teuben 1991). It is noteworthy that *C. richardii* had the greatest effect on soil K concentrations and they were the species producing the most faeces (A.-M. Smit and R. J. van Aarde, personal observation). The fact that elements other than NH^{4+} and NO^{3-} were not significantly different between controls and experiments with very low concentrations overall in the soil, may be due to the fact that the experiment was run over a short period and some elements such as P take longer to accumulate in the soil. Note that species-specific differences are in some instances exemplified through some sex-specific differences. Our results have illustrated that this is the case in particular for Mg concentrations. In general though, sex-specific influences were negligibly small (refuting hypothesis 3) and also related to species-specific differences. We could therefore safely ignore these sex-specific differences for the remainder of the analyses.

Changes in biomass did not cause predictable changes in P, N and C concentrations. However, 5–15 g of millipedes resulted in the highest concentrations of Mg and K. It was therefore decided to use 5–15 g of millipedes in Phase III to ensure that changes in soil element concentrations related to millipede activity could be detected, yet at the same time account for biomass effects on Mg and K.

The results illustrated that compositional effects (both for one and two species) resulted in differential rates of change for K. This supported our earlier findings in Phase I where the presence of *Spinotarsus* sp. resulted in higher rates of change than the other species. However, some anomalies exist with Phase I recording higher rates of change for P, Mg, N and C in the presence of *Spinotarsus* sp. compared with the other species, while Phase III recorded no significant differences. We believe that some inherent seasonal differences (Phase I was conducted during February and March while Phase III was conducted during November) in millipede behaviour may account for these results as invertebrates are often characterized by fixed seasonal behaviour patterns (Engelmann 1970). Nevertheless, our results suggest that species composition may have significant influences on the rate of change in soil element concentrations due to species-specific differences already highlighted in Phase I.

Our results also compare favourably with studies on the influence of soil animal community complexity on primary productivity (Mikola & Setälä, 1998; Laakso & Setälä 1999). Laakso & Setälä (1999) concluded that primary productivity is insensitive to variation in complexity at species as well as trophic level. Symstad *et al.* (1998) similarly found that the effect of losing a single species on productivity and nitrogen retention in grasslands depends on the characteristics of the species and the ecosystem. It would therefore appear that in some ecosystems species-specific properties are more important in affecting nutrient cycles than the species number *per se*.

Overall, how do our results reflect on the four hypotheses constructed by Lawton (1994)? In essence we have support for all four hypotheses. Rates of change in P, Mg and C probably reflect on the null as well as idiosyncratic hypothesis. Rates of change in P and Mg remained constant with an increase in richness (null hypothesis) while that of C was unpredictable (idiosyncratic hypothesis). Rates of change in K reflect on the rivet hypothesis (rate of change increased with an increase in richness), whereas rates of change in N reflect on the redundancy hypothesis (rate of change increased initially but did not change at higher richness). We believe that variable species-specific effects have the potential to generate patterns that will support all four hypotheses depending on the species involved and the components of ecosystem function that are being measured.

In conclusion, the activity of all three species *C. fulgidus*, *Spinotarsus* sp. and *C. richardii* increases the concentrations of selected elements in the soil substrate. However, the rate at which they affect the concentrations of these elements in the soil substrate suggests different roles within this functional group. Apparent relationships of rates of change with millipede richness are a result of compositional effects, which reflect species-specific effects on rates of change in concentration of soil elements. Nevertheless, the rate at which these soil elements increase in the microcosms suggests that millipede activity may accelerate the release of elements such as P, Mg, K, N and C in areas of coastal sand dunes undergoing vegetation regeneration. The accelerated release of these elements in dunes undergoing vegetation regeneration will contribute to ecosystem recovery following mining.

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