Faunal changes along a vegetation gradient in the Alexandria Coastal Dunefield, South Africa

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Coastal dunes are distinguished by their border with the sea and the resultant abiotic and vegetation gradients perpendicular to the shore. This study, conducted in the Alexandria dunefield, tested the prediction that faunal community changes along a dunefield gradient reflect successional changes in vegetation structure. Three sites at increasing distances from the shore were examined: a vegetated dune slack, a bushpocket and dune thicket. Vegetation complexity increased inland, although the slack and pocket were similar. Arthropod and small mammal richness and diversity were highest in the thicket and lower, but similar, in the slack and bushpocket. Avifaunal species richness increased away from the sea. The results support the hypothesis of faunal response to vegetation structure changes.

Kusduine word gekenmerk deur hul grens met die see en die gevolglike gradient in fisiese faktore en plantegroei loodreg met die kus. Die huidige studie, onderneem in die Alexandria duineveld, het die volgende hipotese getoets: veranderinge in dieregemeenskappe oor so 'n gradient word bepaal deur veranderinge in plantegroeistruktuur. Drie habitatte is gekies op toenemende afstande van die kus: laagliggende holte met pionierplante; duinebos; en hoë bos agter die duine. Plantegroeistruktuur het meer kompleks geraak weg van die see alhoewel die holte- en die duinebosgemeenskappe baie eenders was. Die spesiesrykheid en -diversiteit van Arthropoda en klein soogdiere was die hoogste in die hoë bos en laer (maar soortgelyk) in die duinebos en holte. Voëlverskeidenheid het toegeneem weg van die see. Hierdie bevindinge ondersteun die hipotese dat dieregemeenskappe deur die plantegemeenskap-struktuur bepaal word.

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The Alexandria Coastal Dunefield in the Eastern Cape is the largest uninterrupted and active coastal dunefield in South Africa (Tinley 1985) and is made up of a massive transgressive sheet of reversing transverse dunes (McLachlan, Sieben & Ascaray 1982; McLachlan, Ascaray & du Toit 1987). The most distinctive feature of coastal dunes is their border with the sea and the resultant physical, chemical and vegetation gradients perpendicular to the shoreline (Ardö 1957; McLachlan 1991). For this reason, dune studies have often concentrated on vegetation succession along this gradient (Ardö 1957; Cotton 1967; McLachlan *et al.* 1987; Avis 1992). McLachlan *et al.* (1987) demonstrated vegetation succession from east to west within a coastal dune slack in the Alexandria dunefield. However, the dune vegetation also exhibits a clear succession from a pioneer community near the beach to a stable climax community inland (Parker-Nance, Talbot & Bate 1991). Tinley (1985) has defined four vegetation zones in South African coastal dunes — pioneer, shrub, thicket and forest. This study focused on the first three of these vegetation types. Since habitats within dunes have been found to be more significant than dune form in influencing animal distribution (Duffey 1968; Caussanel 1970), this study aimed at testing the prediction that faunal changes along a dunefield gradient perpendicular to the beach reflect changes in vegetation structure.

Study area

The Alexandria Coastal Dunefield (Figure 1) (33°44'S; 25°51'E) is 6000 years old and occupies a total area of 120 km^2. Acted on by the dominant south-westerly winds, overall sand movement is north-eastwards, resulting in sand transport almost parallel with the shore and dune movement at a rate of 4–5 m/year (McLachlan *et al.* 1982). The dunefield is largely

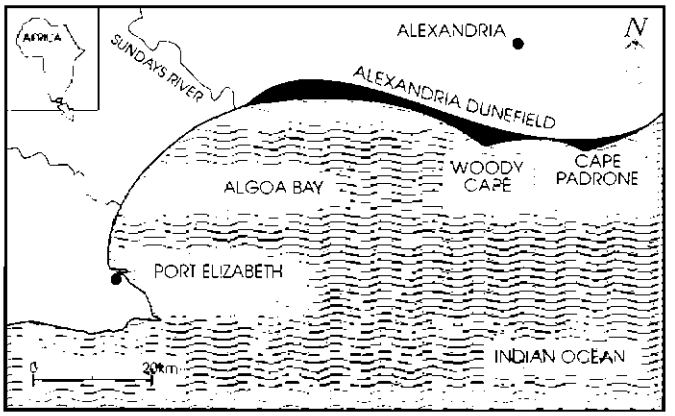

Figure 1 The study site in the Alexandria Coastal Dunefield.

unvegetated, but includes some specialized habitat types (McLachlan *et al.* 1987). Three of these were surveyed annually over five years (1987–1993): a vegetated dune slack representing the transition between pioneer and shrub community with groundwater close to the surface (Site 1), a bushpocket near the landward margin of the dunefield (Site 2) and a dune thicket community near the main slip face representing the climax community (Site 3) in this area, since low rainfall (400 mm p.a.) precludes development of forest (Tinley 1985). The pioneer community of the dune slack is maintained at this seral stage by wind and sand movement.

Methods and Materials

Vegetation complexity

Since vertical stratification of vegetation increases with maturity, horizontal vegetation density at different heights was

used as an index of vegetation complexity. The horizontal density of the vegetation was determined using a density board (at 20-cm intervals from 0–2 m, thereafter at 100-cm intervals) following MacArthur & MacArthur (1961). The distance from the point at which 50% of the board was obscured by vegetation on a horizontal plane was measured in the four cardinal directions for each height class. The reciprocal of this distance is directly proportional to foliage density within that height class (MacArthur & MacArthur 1961). Complexity was further indexed as the percentage vegetation cover of the various growth forms present at each site, using a point intercept method (Mueller-Dombois & Ellenberg 1974) for 500 point intervals over 50 m randomly selected transects, and recognizing six categories: sand, litter, grass, forb, shrub (> 1 m) or tree (> 2 m). The above-mentioned measurements were taken annually over a five-year period.

Fauna

Faunal samples were collected over 48 h annually for five years. Pit traps were used to collect arthropods (insects and arachnids). Sites 1 and 2 comprised one line of 10 traps placed approximately 5 m apart, while Site 3 comprised two lines of five traps set 5 m apart. The traps were cleared at dawn (06h00) and dusk (18h00) and the captured arthropods identified to the level of Order. Bird species present at each site (excluding transients such as swallows) were recorded in the morning and again before sunset. Numbers of birds were not recorded. Small mammals were trapped using Sherman live traps baited with a mixture of oats and peanut butter. Five trap lines, each comprising 10 traps placed at 5-m intervals, were placed 5 m apart over two nights, yielding a total of 100 trap sessions per site per year. Traps were checked at 06h00, 12h00 and 18h00 and the captured animals weighed, sexed, identified and released.

Statistical procedures

Analyses of variance were performed to elucidate differences in the vegetation and faunal species composition between the three sites (no statistics were performed on avifaunal data, as numbers were not collected). Kruskal-Wallis analyses of variance were used for non-parametric data and proportional data were arcsine transformed (Zar 1984). Degrees of freedom reported are between groups. Statistics were not attempted on the small mammal data, as very low numbers were trapped. Diversity of vegetation cover, arthropods and small mammals was estimated as the Shannon-Wiener information theory index (Pielou 1975).

Results

Vegetation complexity

The slack and pocket sites (Sites 1 & 2) had very similar vegetation cover at ground level, as well as sparse and low canopies (Figure 2). In contrast, the thicket site (Site 3) displayed considerable horizontal vegetation densities between the ground and 0,8 m, and also the highest canopy. The study sites exhibited clear differences in the compositions of their vegetation (expressed as % cover) (Figure 3). The slack community consisted mainly of shrubs, forbs and litter, with very little grass, whereas the bushpocket was dominated by shrubs

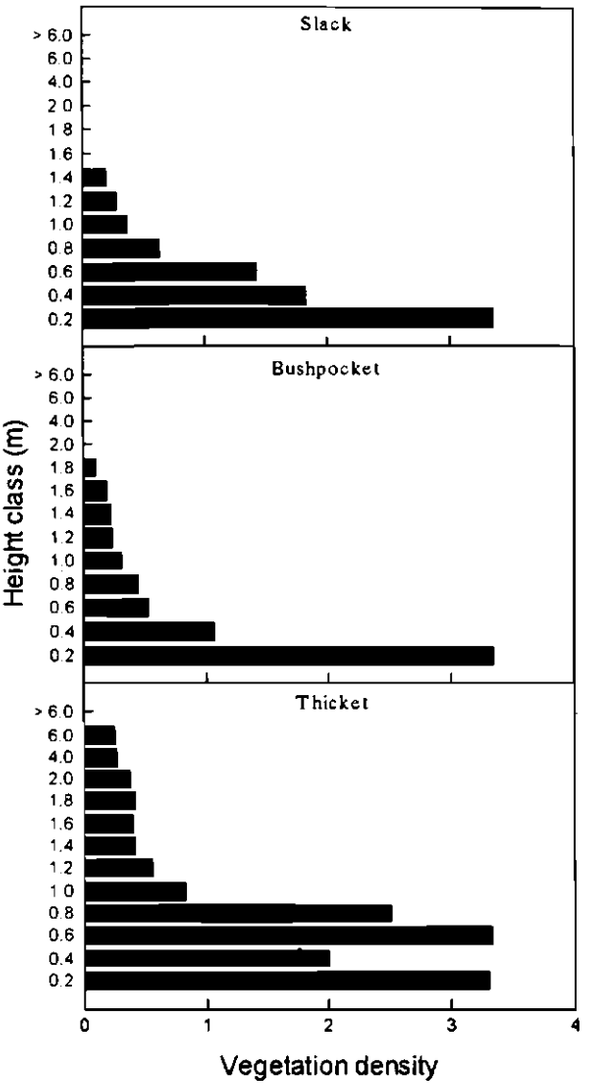

Figure 2 Vegetation density profiles of the slack, bushpocket and thicket communities in the Alexandria dunefield.

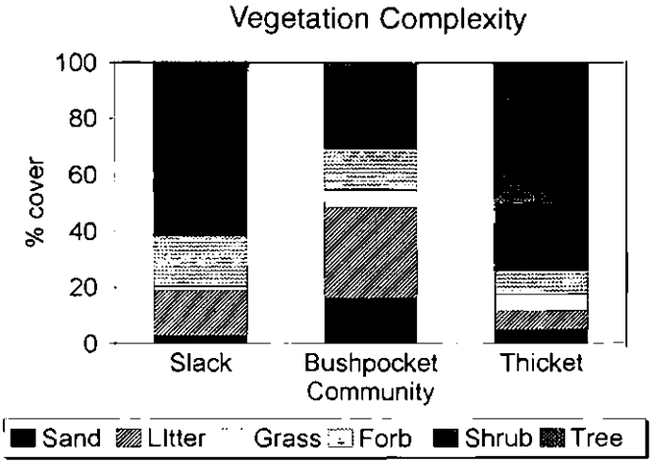

Figure 3 Vegetation growth forms (% cover) at the three sites along a shore-normal gradient in the Alexandria dunefield.

and litter, with sand and forbs present to a lesser extent and very few trees. In contrast, the thicket community was domi

Table 1 Mean arthropod numbers collected in the slack (Site 1), bushpocket (Site 2) and thicket (Site 3) communities over five 48-h periods.

	Slack				Bushpocket				Thicket			
	Day		Night		Day		Night		Day		Night	
Order	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Arachnida	13,0	18,6	8,4	7,2	3,8	2,7	10,6	12,2	3,6	2,7	0,0	0,0
Chilopoda	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	5,6	6,0
Chiloptera	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,4
Coleoptera	9,2	10,5	4,2	7,4	22,2	27,4	1,6	1,9	10,4	8,4	0,0	0,0
Collembola	1,6	3,2	5,6	11,2	0,2	0,4	1,2	2,4	0,8	1,6	1,2	1,5
Dermaptera	0,0	0,0	0,2	0,4	0,0	0,0	0,2	0,4	0,2	0,4	1,0	1,5
Diplura	0,2	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Diptera	4,6	3,7	1,2	1,9	3,2	2,8	0,8	1,6	5,0	2,4	0,0	0,0
Ephemeroptera	1,4	2,8	7,2	14,4	0,0	0,0	0,8	1,6	1,0	2,0	1,4	2,0
Hemiptera	0,4	0,5	0,8	1,6	0,2	0,4	0,4	0,8	0,0	0,0	4,2	8,4
Homoptera	0,4	0,8	0,0	0,0	0,6	1,2	0,2	0,4	0,2	0,4	0,2	0,4
Hymenoptera	40,6	37,8	60,4	91,1	20,2	20,6	18,0	24,6	10,4	12,3	0,6	0,8
Isoptera	0,0	0,0	0,2	0,4	0,2	0,4	0,2	0,4	0,0	0,0	2,4	2,0
Mallophaga	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,4	0,0	0,0
Neuroptera	0,0	0,0	1,0	2,0	0,0	0,0	0,0	0,0	0,2	0,4	0,2	0,4
Odonata	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,4	0,4	0,8
Orthoptera	1,2	1,2	0,6	0,5	1,0	1,1	0,4	0,5	1,8	2,1	0,0	0,0
Protura	0,2	0,4	0,2	0,4	0,2	0,4	0,0	0,0	0,0	0,0	1,0	1,1
Pseudoptera	0,2	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Siphonaptera	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,4	0,0	0,0	0,0	0,0
Thysanura	22,4	43,3	0,6	0,8	0,0	0,0	1,2	1,9	0,0	0,0	0,0	0,0
Total	13		13		10		13		12		12	
Mean (over 5 yrs)	6,4	2,3	5,4	3,1	5,2	1,5	5,0	3,1	5,8	1,7	4,6	3,0

nated by trees and shrubs, with a similar proportion of grass to the slack community. Analysis of variance revealed that the amount of litter present was lowest in the thicket community (Site 3) and highest in the slack community (Site 1) (F = 19,89; p = 0,0002; *d.f.* = 2). The vegetation at Site 1 consisted of significantly more shrub (F = 10,36; p = 0,002; *d.f.* 2) and Site 3 contained significantly more trees (K = 8,98; p = 0,01; *d.f.* 2). There was no significant difference in the proportions of grass and forbs between sites. The diversity of vegetation growth forms was lowest (H = 1,26) in the slack community and highest in the bushpocket community (H = 1,58), the thicket community having a diversity of H= 1,41.

Fauna

Arthropods

The numbers of arthropods collected over the 48-h periods are presented in Table 1. Although ANOVA revealed no statistically significant differences between the communities, the following results were observed. The slack community was dominated by diurnal Hymenoptera and Thysanura. Collembola and Ephemeroptera also made an important contribution to the slack community, but were largely nocturnal. The bushpocket community was dominated by diurnal Hymenoptera and Coleoptera, but differed in having nocturnal arachnids. Diurnal Hymenoptera and Coleoptera were once again well represented in the thicket, although there was no apparent dominance by any one Order. Diurnal Diptera and nocturnal Chilopoda and Hemiptera were also present at this site. The diversity of Orders of arthropods was highest at the thicket site (H = 2,35) and nearly equal at the slack and bushpocket sites (H = 1,57 and H = 1,53, respectively).

Birds

The number of bird species recorded differed markedly between sites (Table 2). An increase in species richness was observed moving inland, with a total of 12 species recorded in the slack, 32 species in the bushpocket and 58 species in the thicket over the five year period.

Small mammals

The three communities differed in their small mammal compositions. Two species of small mammal were found in the dune slack by day, the community being dominated by *R. pumilio* (Table 3), which had a higher population here than at any of the other sites. This species was also the dominant species caught at night, although in much lower numbers. There were four other species active in the dune slack nocturnally, notably the endemic *Gerbillurus paeba exilis*, which occurred

Table 2 Numbers of bird species recorded in the slack (Site 1), bushpocket (Site 2) and thicket (Site 3) communities over five 48-h periods

Species	Common name	Slack	Bush-pocket	Thicket
Accipiter minullus	Little sparrowhawk			x
Andropadus importunus	Sombre bulbul	x	x	x
Apalis flavida	Yellowbreasted apalis			x
Apalis thoracica	Barthroated apalis	x	x	x
Ardea melanocephala	Blackheaded heron			x
Batis capensis	Cape batis			x
Batis molitor	Chinspot batis		x	
Bostrychia hagedash	Hadeda ibis			x
Bubo africanus	Spotted eagle owl	x		
Burhinus capensis	Spotted dikkop			x
Campethera notata	Knysna woodpecker			x
Caprimulgus pectoralis	Fierynecked nightjar		x	x
Chrysococcyx klaas	Klaas's cuckoo			x
Cisticola fulvicapilla	Neddicky			x
Colius indicus	Redfaced mousebird			x
Colius striatus	Speckled mousebird		x	x
Columba arquatrix	Rameron pigeon			x
Cossypha caffra	Cape robin	x	x	x
Dicrurus adsimilis	Forktailed drongo	x	x	x
Elanus caeruleus	Blackshouldered kite			x
Erythropygia leucophrys	Whitebrowed scrub robin			x
Erythropygia signata	Brown robin			x
Halcyon albiventris	Brownhooded kingfisher			x
Numida meleagris	Helmeted guineafowl			x
Lagonosticta rubricata	Bluebilled firefinch		x	
Lamprotornis nitens	Glossy starling			x
Laniarius ferrugineus	Southern boubou		x	x
Lanius collaris	Fiscal shrike		x	x
Monticola rupestris	Cape rock thrush			x
Motacilla capensis	Cape wagtail		x	
Muscicapa adusta	Dusky flycatcher			x
Nectarinia afra	Greater D-collared sunbird		x	x
Nectarinia chalybea	Lesser D-collared sunbird			x
Nectarinia famosa	Malachite sunbird		x	x
Nectarinia amethystina	Black sunbird		x	
Onychognathus morio	Redwinged starling			x
Oriolus larvatus	Blackheaded oriole			x
Parus niger	Southern black tit			x
Passer domesticus	House sparrow			x
Passer melanurus	Cape sparrow	x		
Phoeniculus purpureus	Redbilled woodhoopoe			x
Phyllastrephus terrestris	Terrestrial bulbul			x
Ploceus capensis	Cape weaver	x	x	
Ploceus ocularis	Spectacled weaver		x	x
Pogoniulus pusillus	Redfronted tinkerbarbet			x
Prinia maculosa	Spotted prinia	x	x	x
Prinia subflava	Tawnyflanked prinia	x	x	x
Pycnonotus barbatus	Black-eyed bulbul		x	x
Pycnonotus capensis	Cape bulbul	x	x	x
Pycnonotus nigricans	Redeyed bulbul		x	
Serinus flaviventris	Yellow canary			x
Serinus gularis	Streakyheaded canary		x	x
Serinus mozambicus	Yelloweyed canary			x
Serinus sulphuratus	Bully canary		x	
Sigelus silens	Fiscal flycatcher		x	x
Spreo bicolor	Pied starling			x
Streptopelia capicola	Cape turtle dove	x	x	x
Streptopelia senegalensis	Laughing dove		x	x
Tchagra tchagra	Southern tchagra			x
Telophorus olivaceus	Olive bush shrike			x
Telophorus zeylonus	Bokmakierie		x	x
Tockus alboterminatus	Crowned hornbill			x
Turdus olivaceus	Olive thrush		x	x
Turtur chalcospilos	Green spotted wooddove			x
Upupa epops	African hoopoe			x
Vidua macroura	Pintailed whydah		x	
Zosterops pallidus	Cape white-eye	x	x	x
Total		12	32	58
Mean (over 5 years)		4,8	13,6	23,6
S.D. (over 5 years)		1,5	1,0	7,4

exclusively at the slack site. The bushpocket community had fewer species than the slack by day (one species) as well as by night (four species); once again *R. pumilio* was dominant. The thicket community included the most (six) nocturnal species. Although *R. pumilio* was the dominant diurnal species at this site, it was present in lower numbers than at the other sites and the nocturnal community was dominated by the insectivorous woodland dormouse *Graphiurus murinus*, which occurred exclusively at this site. The trend exhibited for small mammal diversity appeared to be similar to that of arthropod diversity, in that the thicket community had the highest diversity ($H' = 1,31$) and the slack and bushpocket communities had almost equal diversities ($H' = 0,54$ and $H' = 0,40$, respectively.

Discussion

The three zones investigated exhibited distinct vegetation features, although the dune slack and bushpocket communities were less different from one another than expected. Although most slacks exhibit an increase in vegetation cover away from

Table 3 Small mammals collected in a slack (Site 1), bushpocket (Site 2) and thicket (Site 3) of the Alexandria dunefield over five 48-h periods (values are mean captures per 500 trap sessions)

	Slack				Bushpocket				Thicket			
	Day		Night		Day		Night		Day		Night	
Species	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Rodents												
Aethomys namaquensis	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,4	0,2	0,4	1,6	2,2
Gerbillurus paeba	0,0	0,0	2,8	0,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Graphiurus murinus	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	2,0	2,3
Mastomys natalensis	0,0	0,0	0,2	0,4	0,0	0,0	0,2	0,4	0,2	0,2	1,6	1,4
Mus minutoides	0,0	0,0	0,4	0,5	0,0	0,0	0,6	0,8	0,4	0,3	0,0	0,0
Otomys irroratus	0,4	0,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,25	0,4
Rhabdomys pumilio	25,0	12,3	4,8	4,3	7,8	3,7	2,0	2,1	5,8	3,3	1,0	1,5
Insectivores												
Myosorex varius	0,0	0,0	1,0	1,5	0,0	0,0	0,0	0,0	0,0	0,0	0,2	0,4
Total species #	2,0		5,0		1,0		4,0		4,0		6,0	
Mean sp.# (over 5 years)	1,4		2,8		1,0		1,6		1,0		2,6	
S.D. (over 5 years)	0,5		0,8		0,0		1,0		0,0		1,0	

the sea (McLachlan *et al.* 1987), the study slack was situated landwards of an artificially stabilized area of the dunefield and was thus well vegetated. While the diversity of vegetation cover (i.e. complexity) increased away from the sea, it was slightly lower at the thicket site than at the bushpocket site, owing to the large proportion of trees present, the proportion of shrubs and forbs decreasing inland. The horizontal vegetation densities at Sites 1 and 2 were very similar, once again reflecting the vegetated nature of the slack. The higher canopy at the thicket site (Site 3) is indicative of the climax community in this area under the present low rainfall regime.

Diurnal sand surface temperatures and windspeeds in dunefields tend to be high, creating a hostile environment for dune fauna. However, as one moves away from the sea, the increasing vegetation complexity creates microhabitats of less extreme microclimatic conditions (Callan 1964; Cotton 1967; Kerley, McLachlan & Castley, in press). Because of these harsh conditions, the vertebrate fauna of sand dunes normally comprises mainly reptiles with a few birds and mammals. Arthropods usually dominate the fauna and include crustaceans, spiders and insects (Callan 1964). Although no statistically significant differences in invertebrate numbers could be elucidated, the sites harboured distinct diurnal and nocturnal assemblages. Such distinctive activity patterns are a common adaptation to coastal dune life owing to the harsh microclimates experienced (Ardö 1957; Callan 1964; McLachlan 1991).

Distinct avifaunal communities were associated with the vegetation zones examined, the species richness increasing inland with an increase in the proportion of trees. Although the slack and bushpocket communities had very similar vegetation structures, the slack contained far fewer bird species. This may be explained by the fact that the number of avian trophic guilds increases with increasing average plant height (Brown 1990), the slack comprising lower growth forms. Development of the upper vegetation strata during succession results in the step-wise addition of avian guilds to the community (particularly frugivores) (Brown 1990), thereby increasing the number of species at the thicket site. Plant species occurring in the later stages of dune succession thus rely mainly on birds for seed dispersal (Tinley 1985).

Small mammal community structure is closely linked to habitat structure (Masson & McLachlan 1990; Kerley 1992). This is reflected by the increasing small mammal diversity and richness away from the sea, as well as the fact that the similar slack and bushpocket communities did not differ in small mammal diversity. The vegetation zones examined differed mainly in the proportions of small mammal species present rather than species richness, and it is notable that some species were habitat specialists (e.g. *G. p. exilis* in the slack and *G. murinus* in the thicket) while others exhibited more generalist behavioural patterns (e.g. *R. pumilio*).

Although succession theory predicts an increase in faunal diversity and species richness landwards with the associated vegetation, the higher diversity and richness of arthropods and small mammals at the slack site than in the bushpocket may be explained by the fact that the slack represents an ecotone between primary and secondary dune vegetation communities. A single dunefield will seldom span the entire successional gradient (McLachlan 1991), with all four of Tinley's (1985) zones, and may usually be considered as representing only a part of the total potential gradient. The inland thicket community, representing the climax community under the present low rainfall regime, had the highest diversity and richness of arthropods, small mammals and birds. The study thus supports the hypothesis that faunal changes along a dunefield gradient reflect the changes in vegetation structure.

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