Maintaining diversity through intermediate disturbances: evidence from rodents colonizing rehabilitating coastal dunes

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Abstract

Rodents inhabit the coastal dune forests of KwaZulu-Natal, South Africa. Here habitat rehabilitation following mining of dunes has resulted in coastal dune forest succession similar to that recorded in nonmined forests. We investigated the colonization of rehabilitating stands and evaluate the role of disturbance in maintaining rodent diversity. A trapping programme was established between July 1993 and February 1995 during which rodent colonization, local extinction and species richness were recorded for rehabilitating stands of different ages. Trends in these variables were closely associated with one of three possible outcomes for a disturbed patch over time, with no intervening disturbances following the initial disturbance. Colonization was initially high which led to an increase in species richness. Extinction was lower than colonization, but became higher when the habitat was 3 years old, which led to a decline in richness. We extrapolate this result assuming negligibly small disturbances after the initiation of rehabilitation and suggest that intermediate levels of disturbance maintain rodent species richness in coastal dune forests. Furthermore, our results illustrated species turnover, a prediction of the recorded outcome, with young stands dominated by *Mastomys natalensis* and older stands by *Saccostomus campestris* or *Aethomys chrysophilus*.

Key words: disturbance, diversity, forests, rehabilitation, rodents

Résumé

Il y a des rongeurs dans les forêts des dunes côtières du KwaZulu-Natal, en Afrique du Sud. Là, la réhabilitation de l'habitat après l'exploitation minière des dunes a abouti à une succession de forêts côtières des dunes semblable à celle qui est observée dans les forêts non exploitées. Nous avons étudié la colonisation des endroits en voie de réhabilitation et évalué le rôle des perturbations dans le maintien de la diversité des rongeurs. On a mis au point un programme de piégeage entre juillet 1993 et février 1995, pendant lequel on a noté la colonisation par les rongeurs, l'extinction locale et la richesse en espèces pour les endroits à différents stades de réhabilitation. Les tendances pour ces variables étaient étroitement associées à l'un des trois résultats possibles que peut connaître avec le temps un endroit qui a été perturbé, lorsque aucune autre perturbation ne suit la première. La colonisation a d'abord été forte, ce qui a causé un enrichissement des espèces. Les extinctions étaient moins fréquentes que les colonisations, mais elles ont augmenté lorsque le nouvel habitat a atteint l'âge de trois ans, ce qui a entraîné une perte de richesse en espèces. Nous extrapolons ce résultant en supposant que ce sont de petites perturbations négligeables après le démarrage de la réhabilitation et nous suggérons que des taux moyens de perturbation maintiennent la richesse spécifique des rongeurs dans les forêts des dunes côtières. De plus, nos résultats illustrent une rotation des espèces, une prédiction des résultats rapportés, avec les endroits les plus jeunes dominés par *Mast-*

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omys natalensis et les plus anciens par *Saccostomus campestris* et *Aethomys chrysophilus*.

Introduction

Increased environmental awareness has resulted in numerous efforts directed at determining the consequences of man-induced disturbances for biological diversity (Ehrlich & Mooney, 1983; Schulze & Mooney, 1993; Naeem *et al.*, 1994; Tilman & Downing, 1994). Ecologists have concentrated on theories that can explain the maintenance of diversity (Levin, 1981; Tilman, 1982, 1988; Petraitis, Latham & Niesenbaum, 1989; Tilman & Pacala, 1992), with the majority implicating competition. Although competition has a profound influence on maintaining diversity (Jennions, 1997), processes or mechanisms that eliminate competitive effects are likely to result in variations in species richness on an ecological time scale (Petraitis *et al.*, 1989). At present disturbances are considered as one of the factors that eliminate competitive effects, thereby influencing diversity (see Mooney *et al.*, 1995).

Hypotheses on the exact mechanisms of disturbance that influence diversity can be divided into those involving selective mortality, and those involving catastrophic events causing random, mass mortality (Petraitis *et al.*, 1989). Predation is an example of a disturbance mechanism causing selective mortality, while a volcanic eruption may result in random, mass mortality of a number of species. Selective mortality hypotheses can be seen as equilibrium models where numbers of species stay constant over ecological time. In this case unequal proportions of deaths, where most deaths occur among individuals of a species with superior competitive abilities, release competitive forces allowing the replacement by another species. This has also been referred to as the compensating mortality hypothesis (Connell, 1978).

Catastrophic hypotheses require mechanisms evoking nonequilibrium models. In this case, the competitive exclusion of species is delayed because catastrophic disturbance events routinely set the system back. Diversity is then a result of the frequency of disturbances and the rate of competitive exclusions. If disturbances are too frequent, only a few species that are resistant to continuous disruption remain. If disturbances are too infrequent then patches will approach equilibrium and be dominated by a few species that can competitively exclude others. This suggests that intermediate catastrophic disturbance events will result in the highest species richness (Connell, 1978; Huston, 1979; Petraitis *et al.*, 1989).

The mining of coastal sand dunes and the associated destruction of vegetation on the south-east coast of South Africa can be considered a discrete disturbance event of high intensity resulting in total destruction. The subsequent rehabilitation of these dunes results in coastal dune forest succession (van Aarde *et al.*, 1996), with the development of vegetation communities here being similar to that in nonmined forests (Mentis & Ellery, 1994). The rehabilitating sere represents a system that has experienced a single intense disturbance, with no subsequent man-induced disturbances. Since the regeneration of vegetation communities in the study area represents coastal dune forest succession, it is likely that the colonization of rehabilitating areas by small rodents will be similar to that of habitats resulting from nonman induced disturbances. In the present study we describe colonization of rehabilitating stands by rodents and evaluate the potential role of intermediate disturbance in maintaining rodent diversity by comparing our observed patterns of colonization and extinction with three possible outcomes described by Petraitis *et al.* (1989). Note that we do not evaluate the effect of mining (catastrophic disturbance of high intensity), but use the immediate result as a starting point of no diversity, similar to the starting points used in the models of Petraitis *et al.* (1989). We also describe and compare the resultant rodent communities on different seral stages.

Materials and methods

The study is based on a live trapping programme consisting of 67,130 trapping nights between July 1993 and February 1995 during which 2671 captures of five rodent species were recorded. Bimonthly trapping took place on six permanent trapping grids located on each of five rehabilitating stands of known age. The characteristics of these stands are summarized in Table 1. Trapping grids comprised 49 trapping stations arranged in a 7×7 configuration with 15 m between trapping stations, and were distributed on each stand

Table 1 Description of the characteristics of rehabilitating and nonmined areas of different ecological age identified and used in the present study. The information was extracted from Van Aarde *et al.* (1996)

Age of the habitats in years	Description
0–2-year-old stand (Stand 1)	Rehabilitating area comprising a pioneer community composed of cover crop. Vegetation is low (50 cm) and is characterized by *Sorghum* spp., *Pennisetum americanum, Dactyloctenium germinatum, Zornia capensis* and *Bulbostylis contexa*. Towards the end of the study period the rehabilitating area comprised a simple grassland community with scattered *Acacia karroo* colonizing. Vegetation (70 cm) was characterized by *Dactyloctenium geminatum, Canavalia maritima, Pennisetum americanum* and *Acacia karroo*.
3–5-year-old stand (Stand 2)	Rehabilitating area comprising an *Acacia karroo* shrub land with thick undergrowth dominated by grass species. The vegetation is characteristically 1–1.5 m high with *Acacia karroo* and *Dodonea angustifolia* the most prominent woody species and *Chrysanthemoides monolifera* and *Passerina rigida* occurring frequently. The ground cover consists of *Dactyloctenium germinatum, Canavalia maritima, Bulbostylis contexa* and *Mariscus dubius*.
6–8-year-old stand (Stand 3)	Rehabilitating area comprising an *Acacia karroo* scrub land or thicket with sparse undergrowth with the vegetation characteristically 1.5–3 m high. *Acacia karroo* dominates the canopy while some *Dodonea angustifolia* is still present. The middle stratum, although very sparse is characterized by *Eugenia capensis, Carrisa bispinosa* and *Brachylaena discolor*. The ground cover is sparse and consists mainly of *Dactyloctenium germinatum*.
9–12-year-old stand (Stand 4)	Rehabilitating area comprising Acacia *karroo* woodland with few secondary dune forest species present. This area is characterized by the vegetation being 3–8 m high. The canopy is dominated by *Acacia karroo* while a number of other woody species including *Brachylaena discolor and Vepris lanceolata* are also present. Ground cover consists primarily of *Microsorium scolopendrium* and *Brachiaria chusqueoides*.
13–15-year-old stand (Stand 5)	Rehabilitating area comprising an *Acacia karroo* woodland, 9–12 m high and characterized by secondary dune forest tree species colonizing. These include *Trichelia emetica, Trema orientalis, Mimusops caffra, Brachylaena discolor, Celtis africana, Vepris lanceolata, Albizia adiantifolia, Kraussia floribunda* and *Apodytes dimidiata*. Climbers include *Sarcostemma viminale* and *Andenia gummifera* with *Asystasia gangetica* making up most of the woodland groundcover. Very little grass is present and is represented by *Brachiaria chusqueoides*.
30–35-year-old stand of nonmined forest	Nonmined areas comprising a secondary coastal dune forest with the canopy, 12–15 m or higher, dominated by *Acacia karroo*. Other important canopy trees include *Celtis africana, Mimusops caffra, Allophylus natalensis, Teclea natalensis* and *Ochna natalita*. The middle stratum consists of species such as *Ochna natalita, Clausena anisata, Diospyros natalensis, Tricalysia sonderana, Carissa bispinosa* and *Maytenus undata*. I*soglossa wooddii* and *Dracaena hookerana* dominate the herb and shrub layer.
Stand of nonmined forest of unknown age (Zulti North)	Nonmined area comprising a secondary coastal dune forest with the canopy, 12–15 m or higher. A number of species are abundant, which include *Celtis africana, Mimusops caffra, Allophylus natalensis, Teclea natalensis* and *Ochna natalita*. The middle stratum consists of species such as *Ochna natalita, Clausena anisata, Diospyros natalensis, Tricalysia sonderana, Carissa bispinosa* and *Maytenus undata*. I*soglossa wooddii* and *Dracaena hookerana* dominate the herb and shrub layer.

in such a way that the maximum distance was obtained between them.

Six trapping grids of similar dimensions were also established on a 30–35-year-old stand of nonmined forest during June 1994 and trapping was conducted here during June and September 1994. Access to these trapping grids was difficult as a result of ongoing mining operations resulting in only three of the trapping grids here being trapped during February 1995. Three trapping grids were also established on an apparently mature stand of nonmined forest of unknown age and trapped during September 1994 and February 1995.

Trapping sessions lasted for 5 consecutive days and nights using Sherman Live Traps baited with rolled oats and peanut butter. Rodents were captured and released after being marked and their sex and weight determined. Estimates of species-specific densities (individuals ha^{-1}) were based on the minimum number of individuals alive during each trapping session and corrected for the area covered by the trapping grids. No immigration, emigration or birth and death were assumed during each trapping session as well as no edge effect. Total rodent densities were calculated by summing species-specific densities. No seasonal variation in densities was recorded (S.M. Ferreira, pers. obs.) and therefore this is not considered in the analysis. This procedure resulted in 198 sets of species-specific density estimates each representing a rodent community, either of known regeneration age, or of a mature nonmined forest. Due to the known date (to the month) of the start of habitat rehabilitation at each trapping grid, more accurate ages could be assigned to each rodent community. Age-classes were therefore also assigned to each at 1-year intervals.

Colonization and extinction rates (expressed as number of species per trapping interval) were determined by counting the number of species appearing or disappearing from one trapping session to the next on the same trapping grid. Species richness was recorded as the number of species captured during a trapping session.

Differences between new age-classes at 1-year intervals in colonization and extinction rates, as well as species richness were investigated using nonparametric Kruskal–Wallis analyses of variance and Mann–Whitney U-tests (Sokal & Rohlf, 1969). Differences between stands in species-specific densities and richness were also investigated using nonparametric Kruskal–Wallis analyses of variance and Mann–Whitney U-tests (Sokal & Rohlf, 1969). Differences in rodent community composition based on densities between stands were investigated using analyses of similarities (ANOSIM). Pair-wise analyses of similarities were conducted to determine which stands differed (Clarke & Green, 1988). Bray-Curtis similarity indices were used as similarity values (Bray & Curtis, 1957) and were calculated as $S_{jk} = 2\,W/(A+B)$, where $W = \Sigma_{i=1}[\min(X_{ij}, X_{ik})]$, $A = \Sigma_{i=1}X_{ij}$ and $B = \Sigma_{i=1}X_{ik}$, where $S =$ the number of species, $X_{ij} =$ the density of species i on trapping grid j, and

$X_{ik} =$ the density of species i on trapping grid k. Significance for all tests was taken at the 95% level.

Results

Five rodent species were recorded during the study occurring on rehabilitating as well as nonmined stands. Both colonization and extinction of rehabilitating stands by rodents did not follow clearly defined age-related trends. Colonization rates did not differ between age-classes (Kruskal–Wallis test: $H_{14} = 21.11$; $P = 0.11$; $n = 159$). Extinction rates were the highest when the habitat was 7 years old and gradually declined thereafter, but rates on the different age-classes did not differ significantly (Kruskal–Wallis test: $H_{14} = 19.14$; $P = 0.24$; $n = 159$) (Table 2). Species richness on the five youngest age-classes was significantly higher than on the other age-classes (Kruskal–Wallis test: $H_{14} = 117.89$; $P < 0.01$; $n = 198$; Mann–Whitney U-tests). However, richness remained relatively constant on older rehabilitating habitats. Age-related differences in richness were reflected in significant differences recorded between stands (Kruskal–Wallis test: $H_6 = 117.78$; $P < 0.01$; $n = 198$) (Fig. 1). Stands 2–5 had significantly lower values than those on a stand of mature nonmined forest (Mann–Whitney U-tests).

Species-specific densities varied greatly between sampling periods on the same stand. In spite of this, the highest densities of multimammate mice, *Mastomys natalensis*, were recorded on Stand 1 and lowest on Stand 4 (Kruskal–Wallis test: $H_6 = 140.20$; $P < 0.01$; $n = 198$) (Table 3). Densities of *M. natalensis* on Stand 2 were similar to those recorded on a stand of nonmined forest of unknown age (Mann–Whitney U-test). Densities for both the pouched mouse, *Saccostomus campestris*, and the red veld rat, *Aethomys chrysophilus*, peaked in nonmined forest of unknown age (*S. campestris*: $H_6 = 31.90$; $P < 0.01$; $n = 198$; *A. chrysophilus*: $H_6 = 82.91$; $P < 0.01$; $n = 198$) (Table 3). Pigmy mouse, *Mus minutoides*, numbers were at their highest on stands 0–5 years old (Stands 1 and 2), and this species was not recorded on Stand 5 or stands of nonmined forest of unknown age (Kruskal–Wallis test: $H_6 = 16,97$; $P < 0,01$; $n = 198$) (Table 3). Angoni vlei rat, *Otomys angoniensis*, was not recorded frequently with highest densities on stands of nonmined forests of unknown age and Stand 1 (Kruskal–Wallis test: $H_{6,} = 40.00$; $P < 0.01$; $n = 198$) (Table 3).

Table 2 Changes in colonization, extinction and species richness (number of species) with increase in habitat age. Mean values were estimated at 1-year intervals and are represented as mean ± standard error

Habitat age	Colonization	Extinction	Species richness
1 years ($n = 6$)	1.67 ± 1.60	0.50 ± 0.55	3.17 ± 0.98
2 years ($n = 4$)	0.75 ± 1.50	0.75 ± 0.96	3.00 ± 1.41
3 years ($n = 3$)	0.33 ± 0.58	1.00 ± 0.00	3.00 ± 1.00
4 years ($n = 4$)	1.25 ± 0.96	1.00 ± 0.82	3.25 ± 0.50
5 years ($n = 4$)	0.75 ± 0.96	0.75 ± 0.96	3.00 ± 0.82
6 years ($n = 0$)	–	–	–
7 years ($n = 4$)	0.50 ± 1.00	1.25 ± 0.96	0.75 ± 0.96
8 years ($n = 5$)	1.40 ± 1.14	1.00 ± 1.41	2.20 ± 1.10
9 years ($n = 4$)	1.00 ± 1.15	1.00 ± 1.15	1.00 ± 1.15
10 years ($n = 0$)	–	–	–
11 years ($n = 5$)	0.40 ± 0.55	0.80 ± 0.84	0.40 ± 0.55
12 years ($n = 6$)	0.67 ± 1.21	0.67 ± 1.21	0.67 ± 1.21
13 years ($n = 4$)	0.75 ± 0.96	0.75 ± 0.96	0.75 ± 0.96
14 years ($n = 3$)	0.67 ± 0.58	0.67 ± 0.58	0.33 ± 0.58
15 years ($n = 4$)	0.50 ± 1.00	0.75 ± 0.96	0.50 ± 1.00
16 years ($n = 6$)	0.33 ± 0.82	0.33 ± 0.82	0.33 ± 0.82
17 years ($n = 3$)	0.33 ± 0.58	0.00	0.33 ± 0.58

Community composition (species and their densities) differed between stands (ANOSIM: $\sigma = 0.285$; $P < 0.01$). Rodent communities on Stands 1 and 2 differed from each other (Table 4), but the variation recorded did not distinguish them from that on stands of non-mined forest of unknown age. Nonetheless, the rodent community on Stand 2 was more similar (ANOSIM: $\sigma = -0.013$) to the community on stands of nonmined forest of unknown age than that on Stand 5 (ANOSIM: $\sigma = -0.088$) (σ of Stand 2 closer to zero). Rodent communities on young stands (Stands 1 and 2) differed from all the other stands, with those of Stands 3, 4 and 5
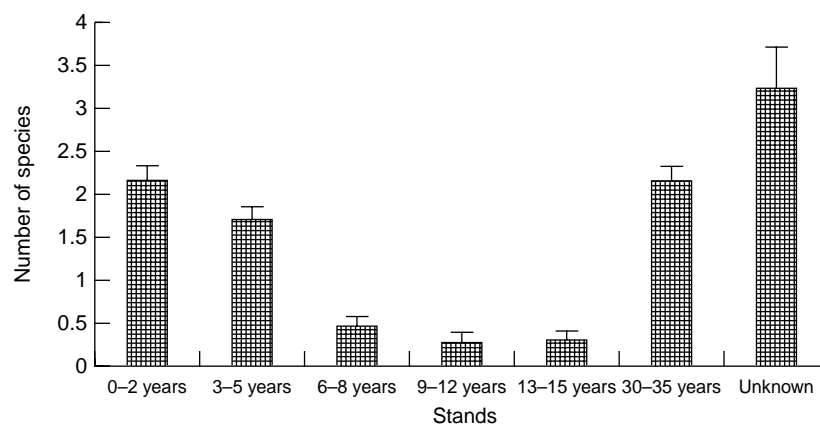

Fig 1 Stand-specific species richness (mean ± SE) of rodent communities recorded during the study period

Table 3 Stand-specific densities (individuals ha^{-1}) recorded for five rodent species on rehabilitating and nonmined dunes. Data are presented as mean values followed by one standard error of the mean. $n =$ number of estimates

	Mastomys natalensis	*Saccostomus campestris*	*Aethomys chrysophilus*	*Mus minutoides*	*Otomys angoniensis*
0–2-year-old stand (Stand 1) ($n = 36$)	25.71 ± 4.90	0.25 ± 0.10	0.91 ± 0.22	0.20 ± 0.07	0.48 ± 0.17
3–5-year-old stand (Stand 2) ($n = 33$)	8.93 ± 1.46	0.63 ± 0.20	0.19 ± 0.08	0.22 ± 0.08	0.06 ± 0.04
6–8-year-old stand (Stand 3) ($n = 38$)	0.65 ± 0.19	0.12 ± 0.08	0.17 ± 0.07	0.05 ± 0.03	0.02 ± 0.02
9–12-year-old stand (Stand 4) ($n = 36$)	0.08 ± 0.04	0.03 ± 0.03	0.13 ± 0.05	0.03 ± 0.03	0.00
13–15-year-old stand (Stand 5) ($n = 33$)	0.11 ± 0.05	0.03 ± 0.03	0.19 ± 0.09	0.00	0.00
30–35-year-old stand of nonmined forest ($n = 15$)	1.46 ± 0.30	0.35 ± 0.22	2.32 ± 0.33	0.05 ± 0.05	0.05 ± 0.05
Stand of nonmined forest of unknown age (Zulti North) ($n = 6$)	9.77 ± 2.08	1.59 ± 0.78	4.77 ± 1.20	0.00	0.68 ± 0.44

similar to each other. Community composition on the 30–35-year-old stand of nonmined forest differed from that on stands of nonmined forests of unknown age.

Discussion

Rodents colonize habitats created by rehabilitation of coastal dune forests, with large variations in colonization and local extinction of individual species. Petraitis *et al.* (1989) suggested that rate of colonization and

extinction of species change as newly disturbed areas age, and that these rates determine the number of species. Using models to predict temporal changes in these rates and their effects on species richness, their analysis suggests that the highest species richness is maintained at intermediate levels of disturbance in accordance with Connell (1978), Lubchenko & Menge (1978) and Huston (1979). This is manifested through a continual setback by intermediate levels of disturbance, and subsequent changes in temporal colonization and extinc-

Table 4 Results of pair-wise analyses of similarities (ANOSIM) between rodent communities occurring on five rehabilitating stands of different ages as well as on a 30–35-year-old stand of nonmined forest and a stand of nonmined forest of unknown age. Communities were compared using Bray–Curtis similarity indices. * = Significant at the 95% level

	0–2-year-old (Stand 1)	3–5-year-old (Stand 2)	6–8-year-old (Stand 3)	9–12-year-old (Stand 4)	13–15-year-old (Stand 5)	30–35-year-old stand of nonmined forest (30 years)	Nonmined forest of unknown age (Zulti North)
Stand 1							
Stand 2	0.044*						
Stand 3	0.324*	0.255*					
Stand 4	0.616*	0.622*	0.107				
Stand 5	0.537*	0.573*	0.038	−0.077			
30 years	0.412*	0.491*	0.241*	0.417*	0.174		
Zulti North	−0.088	−0.013	0.216	0.118	0.418*	0.501*	

tion rates at a specific patch. Petraitis *et al.* (1989) went on to describe three possible outcomes of a disturbed patch over time, with no intervening disturbances following the initial disturbance (see Fig. 2).

The first scenario involves a high colonization rate gradually declining while extinction rate gradually increases with time until both these rates are equal and the number of species stabilizes, but with species turnover. The second involves a decline in colonization rate, while extinction rate initially increases and then decreases until both rates are zero. In this case the

number of species stabilizes and no turnover is observed. In the first two scenarios extinction rate never exceeds colonization rate. The third scenario involves a decline in colonization rate, an initial increase in extinction rate until the latter becomes higher than the colonization rate, after which it declines until the two rates are equal, but not at zero. The consequent result is an increase in species richness followed by a decline after which it stabilizes at a lower level. Should intermediate levels of disturbance maintain the highest number of species, only the third sce-
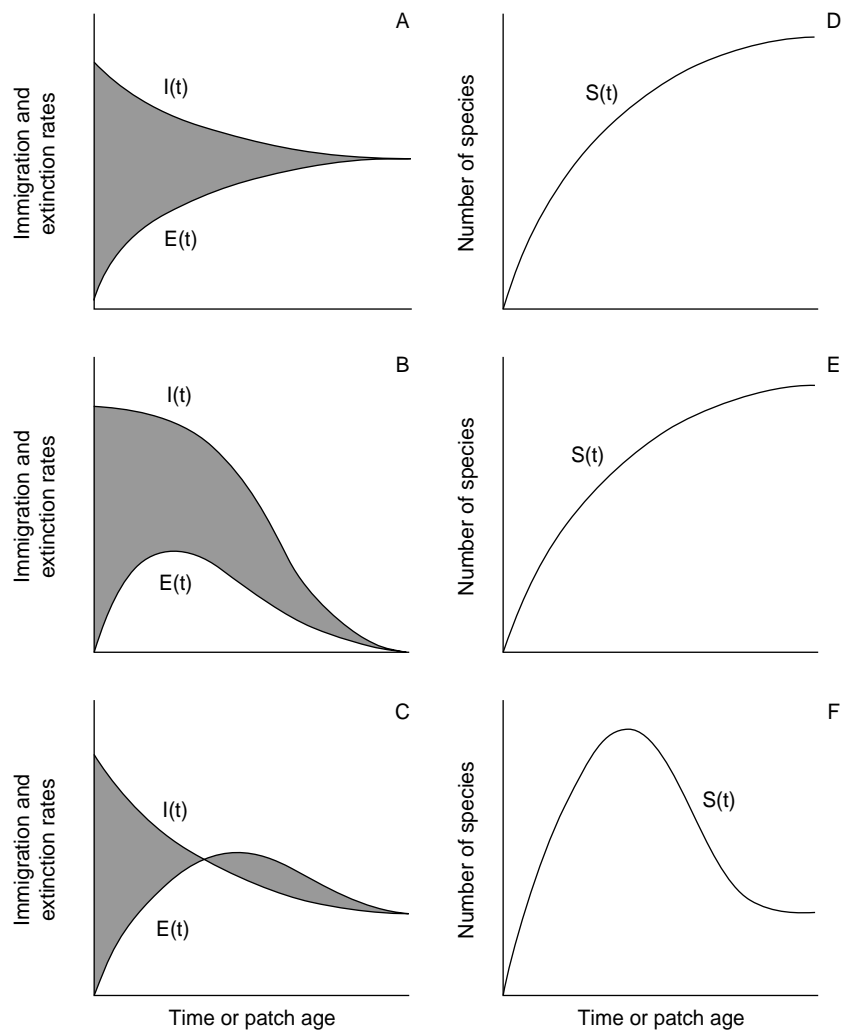

Fig 2 Temporal changes in colonization, extinction and species richness following a disturbance event (from Petraitis *et al.*, 1989). Immigration is the same as colonization. The number of species (S(t)) is the integral of the difference between the rates of colonization (I(t)) and extinction (E(t)). Where E(t) is greater than I(t), as in C, there is a decline in species number. When E(t) and I(t) are matched, the system is at equilibrium. A and C are open to colonization, but B is not

nario would result if no further disturbances were allowed.

The colonization and extinction rates of rodent communities in rehabilitating and nonmined coastal dune forests did not follow clear patterns with an increase in stand age. However, species richness initially increased, and subsequently declined, with stand age on rehabilitating stands. This is in accordance with the third scenario outlined by Petraitis *et al.* (1989) (Fig. 2). Mining of sand dunes is a discrete disturbance event, and the development of vegetation communities on rehabilitating stands represents coastal dune forest succession (Mentis & Ellery, 1994). Thus it follows that the pattern of change in species richness derived from simultaneously available rehabilitating stands of different ages, represents rodent communities recovering from a disturbance event with no subsequent or negligibly small disturbances. Because this pattern follows a similar pattern as the third scenario of Petraitis *et al.* (1989), intermediate levels of disturbance probably maintain rodent species richness on coastal dune forests in the study area.

Rodent species richness on nonmined areas characterized by patches of forest disturbed by tree-falls forming gaps opening up the forest (Weisser & Marques, 1979) was higher than on rehabilitating areas. Tree falls, for example, at different times create patches that are at different stages of recovery, which may result in patch-localized colonization and extinction rates leading to higher species richness within nonmined areas. These tree falls are likely to represent intermediate disturbance events maintaining rodent species richness in coastal dune forests. In addition, Ferreira & van Aarde (pers. obs.) recorded 3.33 ± 0.33 ($n = 3$) rodent species per trapping grid during 1991 and 3.50 ± 0.50 ($n = 2$) rodent species per trapping grid during 1992 on stands of nonmined forests of unknown age. This is similar to what was recorded during the present study (Kruskal–Wallis test: $H_2 = 0.10$; $P = 0.95$; $n = 9$), suggesting that rodent species richness remained constant in coastal dune forests at least between 1991 and 1995.

The patterns discussed thus far would appear to contradict one another. Mature coastal dune forests are characterized by relatively constant rodent richness over time, but a nonequilibrium model is used to explain these patterns. However, patches within coastal dune forests are characterized by variation in richness over time and space (nonmined forests were characterized by the largest variation in richness between trapping grids for any stand measured at one time) due to changes in colonization and extinction of rodents at these patches. Our results extrapolated from rehabilitating stands suggest that variation in species richness within these patches can be explained by one of the nonequilibrium models of Petraitis *et al.* (1989). The diversity and richness of small mammals within coastal dune forests are a cumulative effect of all patches comprising the forest, and this effect appears to remain constant with time. It is therefore quite likely that local nonequilibrium dynamics lead to regional equilibrium patterns (see Wiens, 1989).

The applicability of the third model of Petraitis *et al.* (1989) to the present study is supported by species turnover during rodent community development on rehabilitating stands. Two rodent species dominated these communities, with *M. natalensis* occurring at high densities on young rehabilitating stands, while *A. chrysophilus* dominated the oldest rehabilitating stands. These results differ from those of Ferreira & van Aarde (1996) who suggested a unidirectional replacement of *M. natalensis* by *S. campestris* during the later stages of habitat rehabilitation. It would appear that *S. campestris* may on occasions reach high densities, and dominate communities during such periods. *Saccostomus campestris* was not recorded at the densities that were recorded by Ferreira & van Aarde (1996) (the highest density recorded then was eighteen animals ha^{-1}).

Mastomys natalensis also dominated small mammal communities on nonmined forests of unknown age during the present study. However, *A. chrysophilus* dominated these stands during 1991 and 1992 (Ferreira & van Aarde, pers. obs.). These results suggest that rodent communities are flexible, with changes in composition of communities with time appearing to be unidirectional during certain periods (1991 and 1992; Ferreira & van Aarde, 1996), but not during other periods (1993–95; present study).

Rodent community composition on rehabilitating coastal dune forests changed directionally with age as a result of the replacement of *M. natalensis* by either *S. campestris* (1991 and 1992; Ferreira & van Aarde, 1996) or *A. chrysophilus* (1993–95; present study). Ferreira & van Aarde (1999) have illustrated that variations in species-specific densities were related to habitat features rather than inter-specific interactions. This mechanism behind species turnover (habitat charac-

teristics) is contradictory to the mechanism proposed by the intermediate disturbance hypothesis (competitive exclusion) (Petraitis *et al.*, 1989). We suggest that intermediate disturbances may maintain rodent diversity in coastal dune forests through the provision of a range of habitat characteristics. Intermediate disturbances therefore provide habitat heterogeneity distributed in a mosaic of patches within coastal dune forests. This result in mature coastal dune forests appears to represent the greatest variability in community composition at local patches. It is likely that the development of rodent communities following disturbances reaches a mature community relatively early during forest recovery. Depending on local environmental conditions, the rodent community may subsequently maintain these mature characteristics at a particular patch, or experience a retrogressive period leading to communities more representative of younger communities at that particular patch. However, these variations exemplify the dynamic nature of rodents in coastal dune forests and illustrate how patch characteristics may influence rodents in coastal dune forests.

Acknowledgements

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