The chronosequence of rehabilitating stands of coastal dune forests: do small mammals confirm it?

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Information on the post-disturbance recovery of biological communities of known age may be used to evaluate costly environmental restoration efforts. When based on data obtained through the instantaneous sampling of sites of different ages, such evaluations will be constrained by the assumption that each of the sampled sites will develop along a similar pathway. We used data collected from June 1991 to February 1995, through a capture-mark-recapture study of small mammals of rehabilitating dune forests on the coast of KwaZulu-Natal, to assess this assumption. Our analyses suggest that the characteristics of small mammal communities of young rehabilitating areas do converge to those of older rehabilitating areas. Developmental changes in community characteristics recorded during 1991/92 were also similar to those recorded during 1994/95. However, year-to-year differences in species composition of especially older rehabilitating stands reflect the dynamic nature of these communities.

Studies as early as 1899 on the vegetation on sand dunes of various ages gave rise to the concept of ecological succession.[1] A formal presentation of ecological succession only appeared during 1916 when Clements presented a primary successional sequence as leading to a regional characteristic, climatically determined, self-maintaining and stable vegetation type. Models of these phenomena have subsequently changed and evolved greatly.[1] Whichever way biologists preferred to think about succession, successional changes remain difficult to quantify due to the time scales involved. Consequently, series of sites of different ages considered to represent successional change have often been used to describe changes in selected community variables during succession.[2,3] Such series of sites have been termed a chronosequence, and are assumed to represent a successional sere.[4]

Analyses based on data obtained at the same time from a series of sites of different successional ages assume that these sites are and have been developing along similar pathways over time. They assume also that the community composition (species present and their density) of a seral stage at time $t + i$ will be the same as that of a consecutive stage at time t, with i being the difference in age of the sites. Spatially separated sites can therefore be equated to temporal responses at a particular site.[5] Miles[6] suggested that demonstrating similarity between spatially separated sites, representing temporal changes, and true temporally separated sites could be a problem. In addition, Austin[7] emphasised that chronosequential analyses disregard climatic fluctuations.

Twigg and co-workers[5] evaluated the use of chronosequence techniques to describe successional changes of small mammal communities along a forested coastal dune system in the Myall Lakes National Park, New South Wales. They showed that the validation of the assumption that spatially separated sites represent temporal changes can be obtained in a relatively short time (five years in their study).

The post-mining regeneration of coastal sand dune vegetation north of Richards Bay in KwaZulu-Natal (28°43'S; 32°12'E) is ascribed to ecological succession.[8–10] The development of the small mammal community is characterised by species addition and replacement, as expected during ecological succession.[11] However, this study[11] and evaluations of the progress of post-mining rehabilitation by Richards Bay Minerals in the study area[12,13] assume that sites of different ages represent a chronosequence. In the present paper we investigate the chronosequence assumption using data on small mammals (rodents and shrews) collected over a
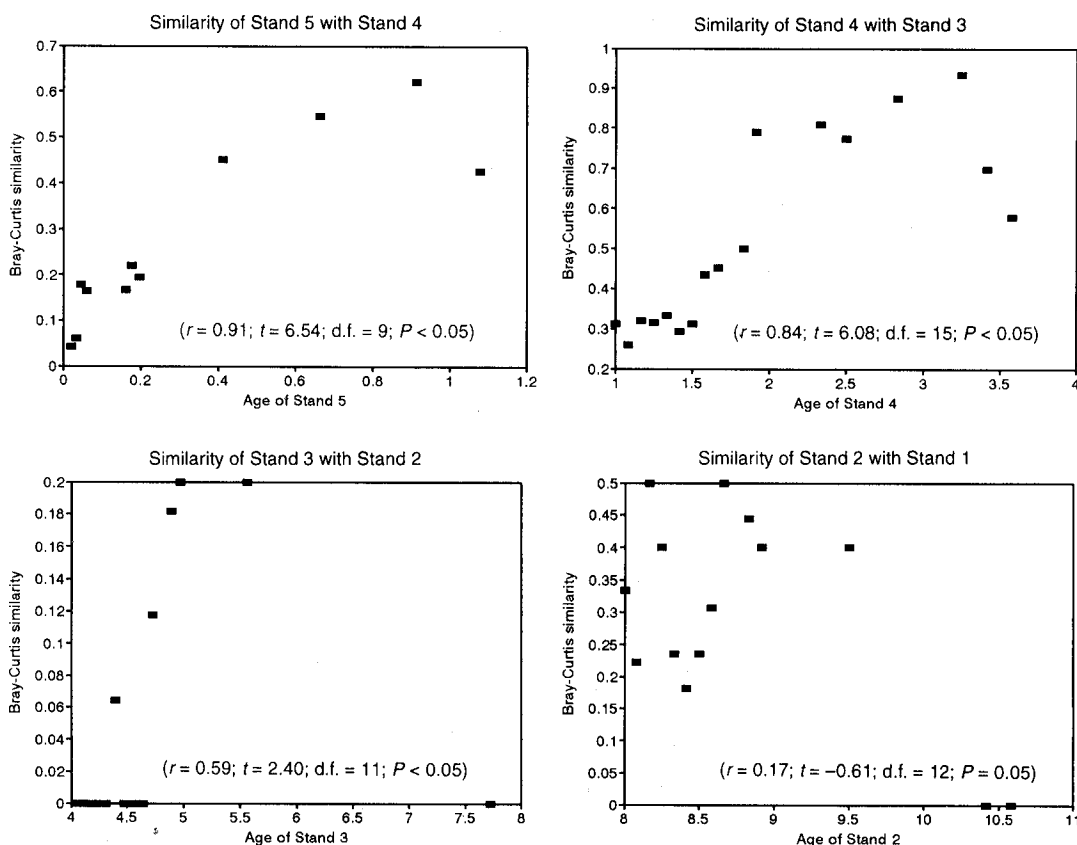

Fig. 1. Changes in the similarity of Stands 2, 3, 4 and 5 in relation to the youngest sampling point of Stands 1, 2, 3 and 4, respectively. The *x*-axis represents stand age in years, *r* is the Spearman-rank correlation coefficient, and *t* is the *t*-value.

Table 1.   Summary of the vegetation characteristics of five stands during 1991/92 and 1994/95. The years during which rehabilitation was initiated on each stand are presented in parentheses.

	1991/92	1994/95
Stand 1 (1978–80)	The plant community was dominated by *Acacia karroo*, with several other indigenous species taking root, these including *Brachylaena discolor, Tricalysia sonderiana, Canthium inerme* and *Carissa bispinosa*.[8] Climbers included *Sarcostemma viminale* and *Adenia gummifera*, with *Ipomoea* spp., *Microsorium scolopendrium, Brachiaria chusqeuoides* and *Asystasia gangetica* making up most of the woodland ground cover.[21] Eleven to 13 years old.	Area comprised an *Acacia karroo* woodland, 9–12 m high and characterised by secondary dune forest tree species colonising. These included *Trichelia emetica, Trema orientalis, Mimusops caffra, Brachylaena discolor, Celtis africana, Vepris lanceolata, Albizia adiantifolia, Kraussia floribunda* and *Apodytes dimidiata*. Climbers included *Sarcostemma viminale* and *Adenia gummifera* with a *Digitaria diversinervis* making up the most important part of the woodland groundcover.[13] Fourteen to 16 years old.
Stand 2 (1981-84)	The plant community was dominated by *Acacia karroo*, which was much more dense than on Stand 1. Other species include *Brachylaena discolor* and *Vepris lanceolata*. Ground cover was not as extensive as in stand 1 and consisted mainly of *Microsorium scolopendrium* and *Brachiaria chusqueoides*.[21] Seven to 10 years old.	Area comprised an *Acacia karroo* woodland 3–8 m high with few secondary dune forest species present. The canopy was dominated by *Acacia karroo* while a number of other woody species including *Brachylaena discolor* and *Rhus nebulosa* were also present. Ground cover consisted of a number of species with *Digitaria diversinervis* the most important.[13] Ten to 13 years old.
Stand 3 (1985–87)	*Acacia karroo* dominated the plant community with *Dodonaea angustifolia* also present. Very few *B. discolor* were present with no other indigenous woody species. Ground cover was sparse and consisted mainly of *Dactyloctenium geminatum*.[21] Four to seven years old.	Area comprised an *Acacia karroo* scrubland 1.5 to 3 m high with sparse undergrowth. *Acacia karroo* provided the canopy while some *Dodonaea angustifolia* were present. The middle stratum, although very sparse, was characterised by *Vepris lanceolata* and *Brachylaena discolor*. The ground cover consisted mainly of *Panicum maximum, Digitaria diversinervis, Acacia karroo* seedlings and *Dactyloctenium australe*.[13] Seven to nine years old.
Stand 4 (1988–90)	At the outset of the study stands of exotic grasses such as *Pennisetum glaucum* and *Eragrostis curvula* were prevalent. Later *A. karroo* and *D. angustifolia* were the most prominent species while *Chrysanthemoides monilifera* and *Passerina rigida* occurred frequently.[22] Ground cover was then dominated by dense stands of *D. germinatum* with *Canavalia maritima* also present.[21] One to three years old.	Area comprised an *Acacia karroo* shrubland with thick undergrowth dominated by grass species. The vegetation was 1–1.5 m high and the canopy was dominated by *Acacia karroo* and *Dodonaea angustifolia*, while *Chrysanthemoides monolifera* and *Passerina rigida* occurred frequently. The ground cover consisted of *Dactyloctenium geminatum, Canavalia maritima, Bulbostylis contexa* and *Mariscus dubius*.[13] Four to six years old.
Stand 5 (1991–93)	None present.	Rehabilitating area, which comprised a simple grassland community with scattered *Acacia karroo* colonising. Vegetation (≈70 cm) was characterised by *Dactyloctenium geminatum, Canavalia maritima, Pennisetum americanum* and juvenile *Acacia karroo*.[13] One to three years old.

period of 54 months.

The first hypothesis we derived from the assumption of the existence of a chronosequence is that a community sampled successively on a particular stand of vegetation should converge in similarity to a community sampled on an older stand of vegetation. For example, over three years a community two years old at the time of the first sampling should converge in similarity to a community sampled on a stand five years old at the time of the first sampling. If this hypothesis holds, then the patterns of change recorded any time during the sampling of all the sites should be the same. A second hypothesis has therefore been proposed, which states that successional changes described from data collected during one time period should be the same as those based on information collected during any other time period.

Material and methods

Data on species-specific densities collected by Ferreira and van Aarde[11] and during the present study were considered. During the present study rodents and shrews were captured on five known-age stands of rehabilitating coastal dune forests. The difference in median age of these stands was three years. The vegetation characteristics of these stands are summarised in Table 1. To test the first hypothesis, one trapping grid was located on each stand (Stands 1–4) at the same site as that used by Ferreira and van Aarde.[11] This resulted in these four trapping grids being sampled at one to three-month intervals from June 1991 to February 1995 (54 months). However, only data collected for three years (equivalent to the difference in median age of the stands) from June 1991 were used for this part of the analysis. During the present study, traps were set on trapping grids (trap stations were arranged in a 7 × 7 configuration with 15 m between each) and a trapping session lasted for five consecutive days and nights. Traps were checked at dawn and all individuals captured were weighed, sexed and their breeding condition noted. New individuals were marked (by toe-clipping), recaptures were recorded and individuals were released where captured. Abundance estimates were based on the number of animals marked and converted to density (individuals per hectare) using the areas covered by trapping grids, assuming no edge effects.

The extent of convergence of younger stands into older stands from 1991 to 1994 was assessed using Bray-Curtis similarity indices.[14] This index computes the similarity between communities sampled on two trapping grids, j and k, as $S_{jk} = 2W/(A + B)$, where $W = \Sigma_{i=1}^{S} [\min(X_{ij}, X_{ik})]$, $A = \Sigma_{i=1}^{S} X_{ij}$ and $B = \Sigma_{i=1}^{S} X_{ik}$, with 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. A similarity index was calculated that compared each successive trapping session on a trapping grid on a stand with the first trapping session on a trapping grid on the following older stand. The change in similarity with age was then used as an indication of convergence. Spearman-rank correlation analyses[15] were used to establish if the changes in similarity correlated with age. Significance was taken at the 95% level.

To evaluate the second hypothesis, five

Table 2. Species-specific relative densities (mean ± standard error) on four stands of specific age recorded during 1991/92 and 1994/95, respectively. The results of analyses of similarities (ANOSIM) and Mann-Whitney *U*-tests are presented. ρ denotes the global test statistic of ANOSIM.

Stands 1–3 years old. ANOSIM: $\rho = 0.086$; $P = 0.12$

Species	1991/92 ($n = 8$)	1994/95 ($n = 12$)	$U_{(8.12)}$	P
Mastomys natalensis	0.952 ± 0.011	0.738 ± 0.070	37.50	>0.05
Saccostomus campestris	0.020 ± 0.007	0.00	12.00	<0.05
Aethomys chrysophilus	0.00	0.138 ± 0.049	24.00	>0.05
Mus minutoides	0.005 ± 0.002	0.072 ± 0.035	38.50	>0.05
Otomys angoniensis	0.006 ± 0.002	0.052 ± 0.025	48.00	>0.05
Myosorex varius	0.008 ± 0.002	0.00	18.00	<0.05
Crocidura hirta	0.009 ± 0.004	0.00	18.00	<0.05

Stands 4–6 years old. ANOSIM: $\rho = 0.056$; $P = 0.17$

Species	1991/92 ($n = 9$)	1994/95 ($n = 11$)	$U_{(9.11)}$	P
Mastomys natalensis	0.769 ± 0.066	0.697 ± 0.062	39.00	>0.05
Saccostomus campestris	0.019 ± 0.014	0.161 ± 0.054	27.50	>0.05
Aethomys chrysophilus	0.031 ± 0.014	0.071 ± 0.037	47.00	>0.05
Mus minutoides	0.112 ± 0.042	0.071 ± 0.027	40.00	>0.05
Myosorex varius	0.030 ± 0.016	0.00	33.00	>0.05
Crocidura hirta	0.038 ± 0.028	0.00	38.50	>0.05

Stands 7–10 years old. ANOSIM: $\rho = 0.975$; $P = 0.01$

Species	1991/92 ($n = 9$)	1994/95 ($n = 10$)	$U_{(9.10)}$	P
Mastomys natalensis	0.103 ± 0.038	0.790 ± 0.067	0.00	<0.05
Saccostomus campestris	0.618 ± 0.107	0.00	0.00	<0.05
Aethomys chrysophilus	0.008 ± 0.008	0.168 ± 0.061	25.00	>0.05
Mus minutoides	0.117 ± 0.038	0.017 ± 0.017	19.50	<0.05
Otomys angoniensis	0.00	0.025 ± 0.025	40.50	>0.05
Myosorex varius	0.115 ± 0.055	0.00	25.00	>0.05
Crocidura hirta	0.038 ± 0.026	0.00	35.00	>0.05

Stands 11–13 years old. ANOSIM: $\rho = 0.750$; $P = 0.01$

Species	1991/92 ($n = 9$)	1994/95 ($n = 6$)	$U_{(9.6)}$	P
Mastomys natalensis	0.056 ± 0.029	0.333 ± 0.211	24.00	>0.05
Saccostomus campestris	0.725 ± 0.068	0.056 ± 0.056	0.00	<0.05
Aethomys chrysophilus	0.00	0.556 ± 0.205	9.00	<0.05
Mus minutoides	0.157 ± 0.056	0.056 ± 0.056	17.50	>0.05
Dendromus melanotis	0.037 ± 0.037	0.00	24.00	>0.05
Myosorex varius	0.016 ± 0.016	0.00	24.00	>0.05
Myosorex cafer	0.009 ± 0.009	0.00	24.00	>0.05

additional trapping grids were established on each of Stands 1–4, and six on Stand 5. Trapping procedures here were similar to those described above. This hypothesis was tested by statistically (Mann-Whitney *U*-test[15]) comparing species-specific relative densities (species-specific density expressed as a fraction of total density) on stands of age *t* during the sampling period June 1991–February 1992[11] (referred to as 1991/92) with those of age *t* during the sampling period June 1994–February

1995 (referred to as 1994/95). This three-year interval is equivalent to differences in the chronological age (*i*) of sampled stands. Furthermore, we used analyses of similarities (ANOSIM[16]) to compare stand-age-specific community composition during the two sampling periods. Significance was taken at the 95% level.

Results

Convergence of sites. The similarity of Stand *x* of age *t* with a stand of age *t* + *i*

tended to grow with increase in age of Stand *x* (*x* = 3, 4 or 5), with the correlation coefficients for three of the four data sets investigated being significant (Fig. 1). Due to two outlier values at 10.5 years for the oldest stand investigated (Stand 2), the general trend was that similarity decreased with increase in stand age, albeit not significantly (*r* = –0.17; *t* = -0.61; d.f. = 12; *P* = 0.55).

Comparisons between chronosequences. Species-specific relative densities on Stands 1–3 years old during 1991/92 and 1994/95 were similar for all species but *Saccostomus campestris, Myosorex varius* and *Crocidura hirta*, which were not recorded during 1994/95. Community composition on stands 4–6 years old during 1991/92 and 1994/95 were also similar. However, small mammal community composition on stands 7–10 years old and 11–13 years old during 1991/92 differed from those on stands of similar age during 1994/95. This resulted primarily from differences in relative densities of *Mastomys natalensis, S. campestris* and *Aethomys chrysophilus* (Table 2).

Discussion

The present analyses suggest that small mammal community structures on young regenerating stands (Stands 3, 4 and 5) converge to those of older stands. However, this is not so for older regenerating stands (Stand 2). Furthermore, the results illustrate that instantaneous sampling of young stands (Stands 4 and 5) of different ages at any time yielded data representative of successional changes, whereas on older stands (Stands 2 and 3) this may not be recorded. Twigg and co-workers[5] reported on chronosequences associated with successional changes despite stand age, but pointed out that their analyses should not be taken as a universal validation of the assumption that all chronosequences can be equated to successional changes. The ambiguous results obtained by instantaneous sampling on older regenerating stands during 1991/92 and 1994/95, respectively, highlighted the need for validation of each chronosequence in its own right.

Validated chronosequences should still be interpreted with caution, since responses of species to age-related habitat change may not be linearly related to age. Chronosequences may be influenced by habitat variables characterised by more complex time relationships. Indeed, when one considers *M. natalensis, S. campestris* and *A. chrysophilus* in the present analysis, complex patterns of change in their

relative densities[17] on older stands may have resulted in differences in community composition on these stands between 1991/92 and 1994/95. In spite of low densities from June 1994 to February 1995,[17] the youngest stands during 1991/92 and 1994/95 had the highest small mammal densities[11,17] and similar community compositions, while the oldest stands had the lowest small mammal densities.[11,17] However, community composition on older stands differed between 1991/92 and 1994/95.

Differences between 1991/92 and 1994/95 on these older stands were primarily related to the near absence of *S. campestris* during 1994/95,[17] compared with the numerous captures recorded during 1991/92.[11] The analysis is furthermore confounded by the absence of some species (*Dendromus melanotis, M. varius, Myosorex cafer* and *C. hirta*), recorded in low numbers during 1991/92,[11] during 1994/95.[17] Most biological communities are characterised by a few species occurring at high densities and most present at low densities.[18] The probability of recording a species conceivably declines as densities decrease, so that these four species may seem to have been absent while being present at very low densities. However, the instantaneous sampling of these communities during any of the years studied always revealed the highest *M. natalensis* densities on the youngest rehabilitating stands, followed by either the highest *S. campestris* or *A. chrysophilus* densities on the oldest rehabilitating stands.[11,17]

It is noteworthy that alternative methods have been employed to overcome the time factor involved in successional studies. These include historical reconstruction of successional events[19] and the development of models representing long-term succession.[20] However, few approaches have provided satisfactory results when addressing faunal succession. Given the constraints of these aforementioned methods, the present approach and use of chronosequence analyses may result in a satisfactory description of successional changes on rehabilitating coastal dunes. It follows that the results obtained in the present study suggest that rehabilitating stands of coastal dune forests reflect a true chronosequence of sites and imply that the assumption of chronosequence was not violated.

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