Coastal Dune Forest Development and the Regeneration of Millipede Communities

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Abstract

The rehabilitation of disturbed ecosystems through ecological succession should lead to the recovery of indigenous biological assemblages typical of a region. However, rehabilitation may give rise to unusual successional pathways and lead to atypical assemblages. We compared millipede assemblages along a chronosequence of habitats developing in response to a post-mining coastal dune forest rehabilitation program with those developing spontaneously in the same area. Our comparison suggests that active rehabilitation mimics and even surpasses spontaneous successional development. On both chronosequences, the total number of species, as well as the mean density, diversity, and species richness increased, and dominance decreased, with habitat regeneration age. Moreover, the similarity of millipede assemblages on the two chronosequences to those on three sets of reference sites (mature forests) increased with regeneration age, but this recovery of community composition occurred faster on the rehabilitating chronosequence than on the spontaneously regenerating chronosequence. This suggests that successional processes are leading to a recovery of the predisturbed state, but factors like protection from further disturbances, which occur on the spontaneously regenerating chronosequence, is probably important to ensure success. The distance between a regenerating site and a colonization source area apparently affects the direction of community recovery—assemblages on the rehabilitating chronosequence converged faster onto assemblages on closer reference sites than onto those on reference sites farther away.

Key words: coastal dune forests, millipedes, regeneration, rehabilitation, succession.

Introduction

Restoration of disturbed ecosystems should ideally lead to their transformation from a disturbed state to a state with structure and function similar to that which existed prior to the disturbance (Hobbs & Norton 1996). A complete transformation is seldom attainable (Lockwood & Pimm 1999), and a commonly accepted goal is one of rehabilitation—the reconstruction of an ecosystem that is a self-sustaining entity, requiring minimal or no maintenance or management, but that does not necessarily attain an exact predisturbance species composition (Ewel 1990; Bradshaw 1995). This is usually a significantly easier goal to reach (Lockwood & Pimm 1999), but the regeneration of community structure, including a typical species composition, remains an integral part of the process. Where the recovering habitats are of conservation concern, as is the case with the dune forests of Maputaland in northeastern South Africa (van Wyk 1996), the recovery of community structure and composition is an even more important goal. In rehabilitation programs the regeneration of community structure is often achieved through postdisturbance ecological succession (Bradshaw 1990; Lockwood & Pimm 1999).

However, assemblages developing in response to restoration initiatives may also be influenced by conditions created by the process itself, conditions that may alter the process of natural ecological succession that is typically induced by disturbances. For instance, areas regenerating in response to a rehabilitation action (rehabilitating areas) may either be smaller or larger than those regenerating in response to natural disturbances. This may conceivably be beneficial or detrimental to colonizers and may influence local patterns of colonization and extinction through dispersal limitations and edge effects (Weiermans & van Aarde 2003). Likewise, the geographical distance between the source area and regenerating areas may have a profound and differential effect on the dispersal success of colonizers (Sawchik et al. 2002).

This raises the question of whether assemblages developing in response to rehabilitation are typical for the region or whether they are an artifact of rehabilitation. This may only be established by comparing trajectories of assemblages developing in response to rehabilitation (i.e., human assisted) to those that are spontaneously regenerating (not human assisted). In the present article, we address differences and similarities in the developmental trajectories of millipede assemblages in habitats developing in response to post-mining rehabilitation and those in habitats that are regenerating spontaneously.

We conducted our study on a belt of coastal dune forests in northeastern South Africa. These dunes have a long history of human-induced disturbances ranging from slash-and-burn agriculture to opencast sand dune mining. In spite of these varied disturbances, much of the dune

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forests have remained intact (Weisser & Müller 1983; von Maltitz et al. 1996). These intact areas, our reference sites, represent the predisturbance community composition and can potentially serve as source areas for the colonization of disturbed sites following either the withdrawal of disturbance or the mitigation of disturbance through active rehabilitation (Mentis & Ellery 1994; Ferreira & van Aarde 1996; van Aarde et al. 1996a, 1996b, 1996c; Kritzinger & van Aarde 1998; Lubke & Avis 1999). The mitigation of the disturbance caused by opencast mining comes in the form of an active dune forest rehabilitation program that started during 1978. The rehabilitation process, during which dunes are reshaped to premining topography and covered with topsoil containing the seed of a number of pioneer species, is designed to initiate a natural process of ecological succession (van Aarde et al. 1996a, 1996b, 1996c; Lubke & Avis 1999). After the initial stages, rehabilitation management is limited to wind and fire protection, and the continuous removal of exotic vegetation (van Aarde et al. 1996c). Other disturbed areas in the region are regenerating spontaneously, with the result that a portion of the dune forest cordon comprises a mosaic of dune vegetation patches, of different sizes and in various stages of postdisturbance recovery.

The millipede community occurring on the rehabilitating areas consists of species that colonized the area on their own accord and has developed characteristics similar to those of millipede communities on the undisturbed old forests in the region (van Aarde et al. 1996a, 1996b, 1996c). As part of the present study, we estimated millipede density, diversity, species richness, dominance, and similarity in coastal dune forests regenerating in response to post-mining rehabilitation and in those regenerating spontaneously. We addressed the following questions: (1) How does the development of millipede assemblages on post-mining rehabilitating dune forests compare to that on a series of unmined naturally regenerating forests? (2) Are these assemblages developing toward assemblages typical of undisturbed forests? and (3) How does geographic distance between source areas (reference sites) and post-mining regenerating areas affect the direction of community development?

Methods

Study Area

The narrow belt of coastal dune forests in northeastern South Africa is an ecotype within the Maputaland Center of Endemism and is poorly conserved and managed (van Wyk 1996; van Wyk & Smith 2001). The climate is humid and tropical/subtropical, with an annual average rainfall of 800–1,200 mm (Davis et al. 1994; van Wyk & Smith 2001). The mean annual temperature at Cape St. Lucia station is 21.5°C (Weisser & Müller 1983).

Our study was conducted north of the town Richards Bay (lat 28°47.27′S, long 32°06.57′E), KwaZulu-Natal.

Here we surveyed millipede assemblages on undisturbed, mature coastal dune forest sites (our reference sites) and two sets of regenerating stands that formed the rehabilitating and spontaneously regenerating chronosequences, respectively (Fig. 1). The rehabilitating chronosequence consisted of seven post-mining rehabilitating stands that had been regenerating for 2, 6, 10, 14, 18, 21, and 24 years, respectively, at the time of sampling. The spontaneously regenerating chronosequence consisted of five regenerating stands that were 5, 7, 17, 38, and 54 years old at the time of sampling. The reference sites consisted of three sets of mature forests located between Richards Bay and Cape Vidal (lat 28°8.02′S, long 32°32.85′E) (Fig. 1). The first of the reference sites, the coastal forest strip, is a strip of forest vegetation between the sea and the rehabilitating chronosequence, deliberately left unmined to serve as a source area for colonization. It is located immediately adjacent to the rehabilitating chronosequence, running its full length on the seaward side. The second reference site, the contiguous Mapelane–Sokhulu group, of which the largest part is protected in the Mapelane Dune Forest Reserve, is located about 35 km from the rehabilitating chronosequence. The third reference site, located farthest from the rehabilitating chronosequence (about 60 km), actually consists of a group of five mature forest patches on the eastern shores of Lake St. Lucia, in the St. Lucia Game Reserve. We treated the Mapelane–Sokhulu group and the St. Lucia group as a single forest site each, in the first case because the two forests are essentially one patch, and in the second case because the five St. Lucia patches are all connected to each other through corridors. However, for the analysis of differences in mean community structure (density and diversity), we treated each patch as separate. Together, the three groups of reference sites represent the only significant source areas for the colonization of disturbed sites by forest millipede species.

In order to evaluate whether the distance to the source areas influences community regeneration on the rehabilitating chronosequence, we calculated the distance between the geographic center of each group of reference sites and that of the rehabilitating chronosequence using a 1:10,000 aerial photograph. We could not do this for the spontaneously regenerating chronosequences because the different stands are scattered across the region, whereas the stands of the rehabilitating chronosequence are located close to each other (Fig. 1).

We estimated the ages of the different spontaneously regenerating stands by inspecting several sets of aerial photographs dating from 1937 to 1999. Vegetation recovery on the spontaneously regenerating stands is apparently similar to that of the post-mining rehabilitating stands (Venter 1976; Weisser & Marques 1979).

Data Collection

Surveys were conducted between 0600 hr and 1200 hr from November 2002 to February 2003. On each site,

including all the reference sites, we recorded the number of millipedes of different species occurring on the ground surface, and on plants up to 3 m, in six randomly located sampling quadrats (fixed width of 35 × 6 m). In the Mapelane forest site we sampled four quadrats. In all cases the asymptote of the cumulative species richness curve occurred at fewer than six quadrats per site, indicating an adequate sampling effort. Each sampling quadrat was further divided into 18 blocks of 2 × 6 m and each block into 2 × 2–m subblocks in order to facilitate effective recording of millipedes by four observers. Observers were accompanied, and trained to find and identify individual millipedes, by an experienced field-worker. Quadrats were never closer than 300 m from each other. The different sample sites (but not the quadrats themselves) were surveyed in a random sequence to prevent a systematic weather-induced bias in millipede detection. We identified millipede species on morphological and morphometric characteristics against voucher specimens in our own

collection and those in the Natural Science Museum in Durban, South Africa. Because the taxonomy of millipedes in southern Africa is largely unresolved, we had to place some of the millipedes into morphospecies categories (see Table 1 for authorities and explanations).

Community Variables and Numerical Analyses

For each quadrat, we calculated the density of millipedes (the number of millipedes per 210 m^2), the Shannon–Wiener index of diversity (H'), Margalef's species richness index (d), Simpson's dominance index (D), and the Bray–Curtis similarity to the average composition of each set of reference sites (using log$_e$-transformed abundance data). We calculated H', d, D, and Bray–Curtis similarity using PRIMER v5.

Testing for normality (Kolmogorov–Smirnov test; Legendre & Legendre 1998) and homogeneity of variance (F_{max} procedure; Sokal & Rohlf 1995) preceded all
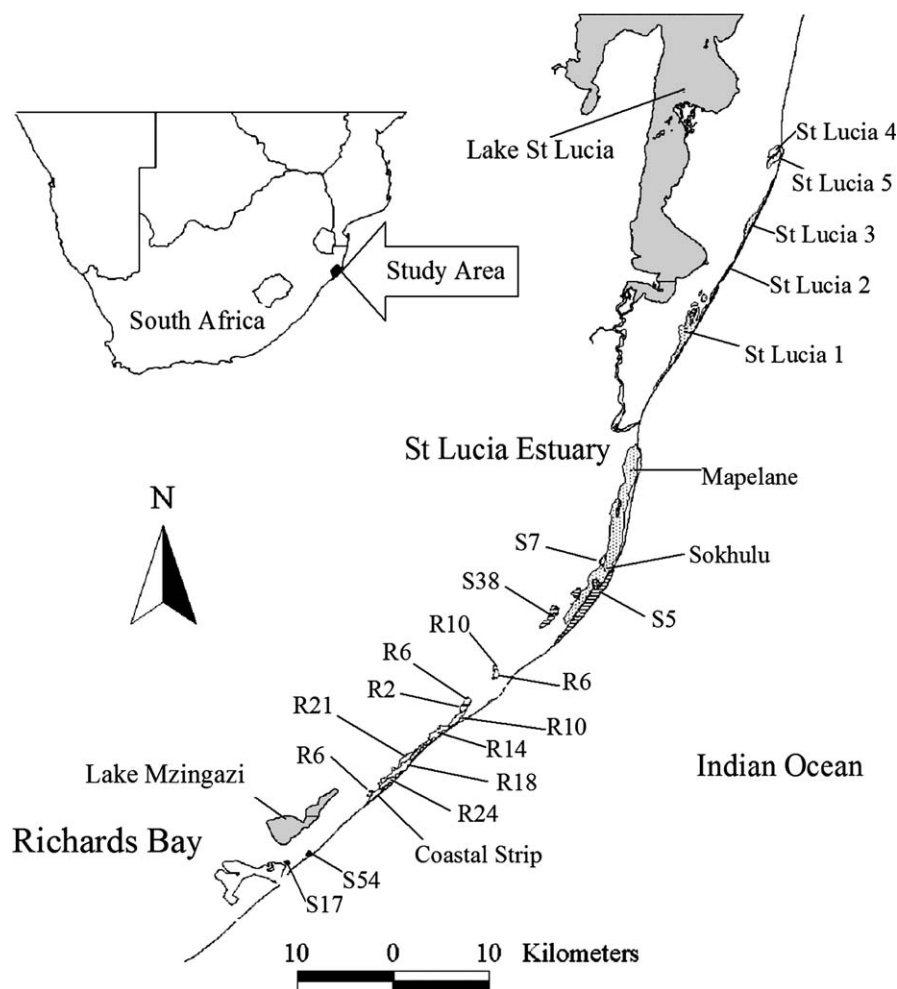

Figure 1. A map of our study sites in northeastern KwaZulu-Natal, South Africa. R2, R6, R10, R14, R18, R21, and R24 indicate sites regenerating in response to post-mining rehabilitation. S5, S7, S17, S38, and S54 indicate spontaneously regenerating sites. The numerical values denote the age (in years) of each of the regenerating sites. The coastal strip, Sokhulu–Mapelane, and St. Lucia (St. Lucia 1–5) are three sets of mature coastal dune forests that were our reference sites for forest development.

Table 1. List of millipede species recorded in different sampling sites.

Species	Author	Post-Mining Rehabilitating Sites (Age in Years)							Spontaneously Regenerating Sites (Age in Years)					Reference (Mature) Sites		
		2	6	10	14	18	21	24	5	7	17	38	54	Coastal Strip	Sokhulu–Mapelane	St. Lucia
Doratogonus sp.	NM?	0	0	1	1	1	1	1	0	1	0	0	1	1	1	1
Orthroporoides pyrocephalus	Koch	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Orthroporoides sp1	NM?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Orthroporoides sp.	NM?	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1
Spinotarsus sp.	NM?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Species 1	NM?	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Centrobolus fulgidus	Lawrence	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Centrobolus richardii	Lawrence	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Centrobolus sp1	NM?	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1
Centrobolus sp2	NM?	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Centrobolus sp3	NM?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Juliformia sp1	NM?	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Juliformia sp2	NM?	0	0	0	1	0	0	1	0	0	0	1	1	1	1	1
Juliformia sp3	NM?	0	0	0	1	1	1	1	1	1	0	0	1	1	1	0
Sphaerotherium giganteum	Porat	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1
Sphaerotherium punctulatum	Brandit	0	0	0	1	1	0	1	1	0	0	0	0	1	1	1
Sphaerotherium sp1	NM?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sphaerotherium sp2	NM?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sphaerotherium sp.	NM?	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
Sphaerotherium sp3	NM?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gnomeskelus tuberosus	Lawrence	0	0	1	1	1	1	1	0	1	0	1	1	1	1	1
Ulodesmus sp.	NM?	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1
Species total number		1	3	6	9	9	7	12	6	7	6	9	12	12	16	19

1 = presence; 0 = absence. NM?—Natural Science Museum, awaiting identification. The St. Lucia site consisted of five forest patches (St. Lucia 1–5) and the Sokhulu–Mapelane group of two contiguous forest patches, of which the Mapelane part is protected. The total number of species for these two reference sites is therefore the sum across all the different patches in each site. The coastal strip is a single, linear strip of forest vegetation between the rehabilitating chronosequence and the beach, running the length of the chronosequence. More detail on species numbers per site is given in Table 2.

statistical analyses. When necessary, we log transformed ($y \rightarrow \ln(y + 1)$) species count data for homoscedasticity (Sokal & Rohlf 1995) and used analysis of variance and Tukey's post hoc multiple comparisons to test for the differences in the mean values of all structural variables. We used least squares linear regression (Sokal & Rohlf 1995) to determine whether the Bray–Curtis similarity of each regenerating site (both chronosequences) to each of the three reference sites increased significantly as site age increased. We used an *F* test (Sokal & Rohlf 1995) to determine whether the rate of change differed between the two chronosequences. We then used analysis of covariance (ANCOVA) (Underwood 1997) to test whether the slopes of these relationships, for the post-mining chronosequence alone, differed according to which set of reference sites was used.

Results

We recorded 17,164 individual millipedes, which we placed into 22 species and morphospecies categories (Table 1). All but one (Species 1) of the species of both the post-mining rehabilitating and spontaneously regenerating sites also occurred in the reference sites (Table 1). Five species (*Centrobolus* sp3, *Sphaerotherium* sp1, *Sphaerotherium* sp2, *Sphaerotherium* sp3, and *Orthroporoides* sp1) from the undisturbed reference sites were not recorded in the regenerating sites (Table 1), presumably because they have not yet colonized these sites.

Density, Diversity, Species Richness, and Dominance

In general, the total number of species, as well as the means of the density ($\log_e$), Shannon diversity, and Margalef's species richness increased, and Simpson's dominance decreased with regeneration age on both the post-mining rehabilitating and spontaneously regenerating chronosequences (Table 2). Particularly for density and Simpson's dominance, the youngest sites on both chronosequences tended to be significantly different from the older sites (Table 2). For diversity, richness, and, to a lesser extent,

dominance, the oldest sites on both chronosequences tended to be significantly different from their respective younger sites (Table 2). For all variables, the oldest sites also tended to be not significantly different from the reference sites (Table 2). The reference sites were significantly different from all younger sites on both chronosequences (for all variables), with the exception of densities on three of the reference sites (Mapelane, St. Lucia 1, and St. Lucia 2), which were similar to values on the youngest sites (Table 2). Some reference sites differed significantly from each other, but there was no consistent pattern in these differences across density, diversity, richness, or dominance (Table 2).

Similarity

Bray–Curtis similarity of each regenerating site to the three sets of reference sites increased significantly with regeneration age, for both chronosequences and regardless of which set of reference sites was used as the reference point (Figs. 2–4). For all three reference sites, the slope for the post-mining rehabilitating chronosequence was significantly steeper than that for the spontaneously regenerating chronosequence (coastal strip, $F_{[1,66]} = 41.03$, $p < 0.001$; Sokhulu–Mapelane, $F_{[1,66]} = 17.24$, $p < 0.001$; and St. Lucia, $F_{[1,66]} = 9.92$, $p = 0.002$).

For the rehabilitating chronosequence at least, the rate at which similarity changed across site regeneration age was dependent on which of the three different groups of reference sites was used as the target. This can be seen in Figure 5, where the slopes of the regression lines in Figures 2–4 (those for the rehabilitating chronosequence) are plotted as a function of the distance between each group of reference sites and the rehabilitating chronosequence. Figure 5 shows that the rate of increase in similarity to the reference site is faster, the closer the group of reference sites is from the rehabilitating chronosequence. The differences between these slopes were significant (ANCOVA, $F_{[2,114]} = 8.46$, $p < 0.001$).

Discussion

Previous work on these post-mining rehabilitating coastal dune forests has shown that plant and animal communities are resilient (Ferreira & van Aarde 1996; van Aarde et al. 1996a, 1996b, 1996c; Kritzinger & van Aarde 1998). Our results support this but also show that rehabilitation-induced changes are apparently typical of natural regeneration processes found in the region. Both community structural and compositional variables changed as the site's regeneration age increased, and these changes were toward values typical of undisturbed forest millipede

Table 2. Structural variables of millipede communities on post-mining rehabilitating sites, disturbed spontaneously regenerating sites, and several undisturbed benchmark sites.

Site	Age (Year)	Area (ha)	Number of Species	Log_e Density	Shannon Diversity	Margalef's Species Richness	Simpson's Dominance
Post-mining rehabilitating sites							
Stand 7	2	32	1	1.51 ± 0.53[h]	—	—	1.00 ± 0.00[a]
Stand 6	6	104	3	5.73 ± 0.36[ab]	0.58 ± 0.07[fgh]	0.20 ± 0.02[g]	0.67 ± 0.08[bc]
Stand 5	10	87	6	6.20 ± 0.21[ab]	0.80 ± 0.02[defg]	0.52 ± 0.04[fg]	0.50 ± 0.02[cde]
Stand 4	14	124	9	4.87 ± 0.20[bcde]	0.75 ± 0.11[efg]	0.84 ± 0.14[defg]	0.62 ± 0.06[bc]
Stand 3	18	80	9	5.29 ± 0.23[abcd]	0.92 ± 0.08[cdef]	0.68 ± 0.12[efg]	0.47 ± 0.04[cdef]
Stand 2	21	190	7	5.52 ± 0.31[abc]	0.89 ± 0.10[def]	0.54 ± 0.07[fg]	0.49 ± 0.06[cdef]
Stand 1	24	76	12	5.14 ± 0.16[abcde]	1.45 ± 0.09[ab]	1.32 ± 0.09[abcde]	0.30 ± 0.03[ef]
Spontaneously regenerating sites							
Site 69	5	535	6	2.55 ± 0.29[gh]	0.75 ± 0.06[fgh]	0.63 ± 0.12[fg]	0.61 ± 0.08[cd]
Site 79	7	34	7	4.23 ± 0.26[def]	0.17 ± 0.05[h]	0.36 ± 0.08[g]	0.93 ± 0.03[a]
Site 07	17	8	6	3.85 ± 0.26[ef]	0.88 ± 0.10[def]	0.70 ± 0.08[efg]	0.51 ± 0.06[cde]
Site 68	38	148	9	4.93 ± 0.32[abcde]	0.29 ± 0.07[gh]	0.51 ± 0.15[fg]	0.86 ± 0.04[ab]
Site 09	54	23	12	5.06 ± 0.2[abcde]	1.49 ± 0.05[ab]	1.70 ± 0.10[abc]	0.32 ± 0.02[ef]
Reference sites							
Coastal strip	Mature	87	12	4.59 ± 0.15[bcde]	1.60 ± 0.09[ab]	1.75 ± 0.11[abc]	0.28 ± 0.03[ef]
Sokhulu	Mature	500	14	4.02 ± 0.20[def]	1.28 ± 0.05[abcd]	1.51 ± 0.13[abcd]	0.36 ± 0.03[def]
Mapelane	Mature	1,670	9	3.69 ± 0.26[efgh]	1.11 ± 0.19[bcde]	1.18 ± 0.24[bcdef]	0.43 ± 0.08[cdef]
St. Lucia 1	Mature	529	11	2.56 ± 0.17[gh]	1.30 ± 0.19[abcd]	1.43 ± 0.29[abcd]	0.33 ± 0.06[ef]
St. Lucia 2	Mature	45	6	3.06 ± 0.30[fgh]	1.23 ± 0.10[abcde]	1.13 ± 0.15[cdef]	0.34 ± 0.03[ef]
St. Lucia 3	Mature	212	10	3.80 ± 0.16[efg]	1.43 ± 0.09[abc]	1.55 ± 0.09[abc]	0.33 ± 0.04[ef]
St. Lucia 4	Mature	75	15	4.84 ± 0.18[bcde]	1.74 ± 0.07[a]	1.99 ± 0.18[a]	0.25 ± 0.02[f]
St. Lucia 5	Mature	106	14	4.38 ± 0.33[cde]	1.68 ± 0.16[ab]	1.93 ± 0.20[ab]	0.27 ± 0.05[ef]

The variables are defined in the text. The results of Tukey's post hoc multiple comparison tests ($p = 0.05$) are also presented. The mean values that share the same letter in a column (across all sites) are not significantly different. Shannon diversity and Margalef's richness could not be calculated for Stand 7 because this site had only one species.
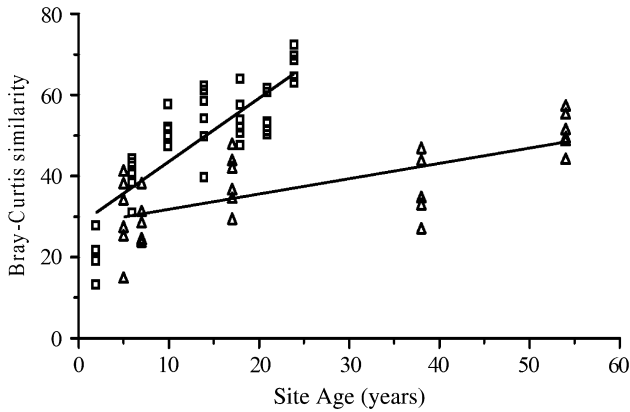
Figure 2. The Bray–Curtis similarity between different-aged regenerating stands and the unmined reference site, the coastal strip. Triangles represent spontaneously regenerating sites, and squares represent those regenerating in response to post-mining rehabilitation. Lines were fitted through least squares regression analyses. The slopes of the lines (1.56 ± 0.17, $r^2 = 0.69$, $F_{[1,38]} = 84.69$, $p < 0.001$ and 0.38 ± 0.07, $r^2 = 0.49$, $F_{[1,28]} = 26.37$, $p < 0.001$ for the post-mining rehabilitating and spontaneously regenerating chronosequences, respectively) differed significantly ($F_{[1,66]} = 41.03$, $p < 0.001$).

communities. Furthermore, community structure (density, diversity, richness, and dominance) on the oldest regenerating sites was never significantly different from that on the reference sites, whereas that on younger sites mostly was. These results suggest that processes leading to recovery of community structure and composition are present, both in sites recovering in response to rehabilitation and in those recovering spontaneously. More importantly perhaps, the rate of community recovery on rehabilitating
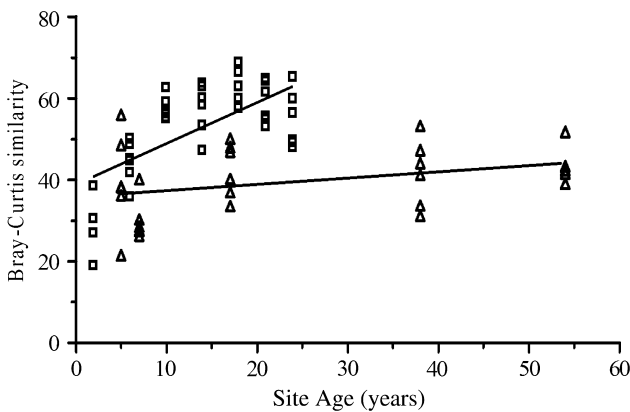

Figure 3. The Bray–Curtis similarity between different-aged regenerating stands and the unmined reference site, Sokhulu–Mapelane. Triangles represent spontaneously regenerating sites, and squares represent those regenerating in response to post-mining rehabilitation. Lines were fitted through least squares regression analyses. The slopes of the lines (1.003 ± 0.19, $r^2 = 0.42$, $F_{[1,38]} = 28$, $p < 0.001$ and 0.16 ± 0.08, $r^2 = 0.12$, $F_{[1,28]} = 3.74$, $p = 0.06$ for the post-mining rehabilitating and spontaneously regenerating chronosequences, respectively) differ significantly ($F_{[1,66]} = 17.24$, $p < 0.001$).
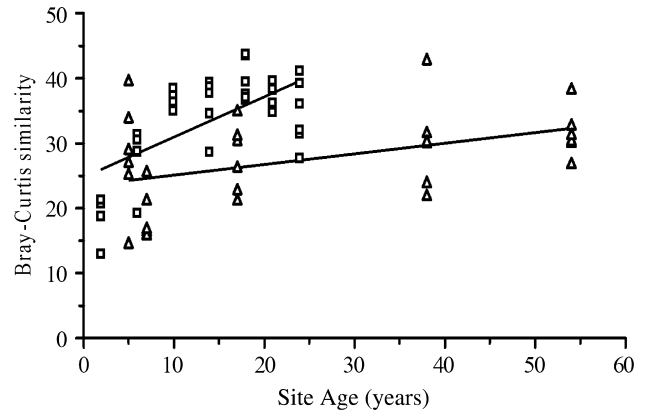

Figure 4. The Bray–Curtis similarity between different-aged regenerating stands and the unmined reference sites at St. Lucia. Triangles represent spontaneously regenerating sites, and squares represent those regenerating in response to post-mining rehabilitation. Lines were fitted through least squares regression analyses. The slopes of the lines (0.62 ± 0.12, $r^2 = 0.41$, $F_{[1,38]} = 26.43$, $p < 0.001$ and 0.16 ± 0.06, $r^2 = 0.19$, $F_{[1,28]} = 6.57$, $p = 0.02$ for the post-mining rehabilitating and spontaneously regenerating chronosequences, respectively) differ significantly ($F_{[1,66]} = 9.92$, $p = 0.002$).

sites exceeded that on sites developing spontaneously, notwithstanding the severity of disturbance through mining. These are important results because they suggest that rehabilitation will not lead to artifactual communities but may be able to re-create the structure and composition of undisturbed communities.
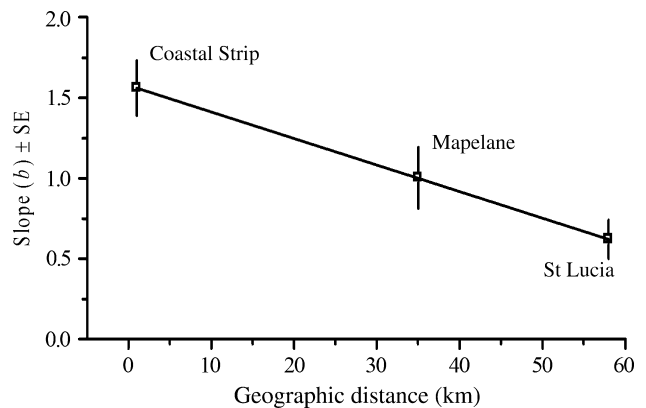

Figure 5. Here we plot the slopes ($\pm$SE) of only the rehabilitating chronosequence regression lines from Figures 2–4, as a function of the geographic distance between the chronosequence and each set of reference sites. The coastal strip is located immediately adjacent to the rehabilitating chronosequence, the Sokhulu–Mapelane forests are located about 35 km away, and the set of St. Lucia sites are about 60 km away. The regression lines from Figures 2–4 describe the change in similarity, across site age, to the three different sets of reference sites. The rate of change in community composition toward a particular reference site is apparently faster, the closer the reference site is to the rehabilitating chronosequence. The line here is fitted for descriptive purposes only. The three slopes plotted here differed significantly from each other (ANCOVA, $F_{[2,114]} = 8.46$, $p < 0.001$).

Our results apparently contradict the generalized assumption that post-mining communities usually take longer to reach a predetermined goal than those developing spontaneously in response to natural succession (Bradshaw 1990). However, the post-mining rehabilitating sites in our study area had two advantages over the spontaneously regenerating sites. First, the limited management interference by Richards Bay Minerals when initiating rehabilitation (Camp 1990) may have benefited the regeneration of the millipede and other communities. The fast development of vegetation (van Aarde et al. 1996a, 1996b, 1996c) played a key role in restoring those conditions that favor colonization by millipedes. Second, the mining company protects the rehabilitating sites from small-scale secondary disturbances such as firewood collection and cattle grazing that may limit development on spontaneously regenerating sites (Wassenaar & van Aarde 2001).

Generalizations about community recovery should however not be made without reference to the specific landscape context of the study area. Our results imply that the millipede assemblages on rehabilitating sites will eventually more closely resemble those on the adjacent coastal strip than those on the other, further reference sites. This may seem self-evident (all else being equal, one may expect closer source areas to provide a larger percentage of the colonizing species), and our estimate of the distances between the source and the rehabilitating chronosequence is necessarily crude. But all else is never truly equal—the distance to source may vary from crucially important in one taxon to being a minor factor in another (Rhainds et al. 2002; Sawchik et al. 2002). Even within a taxon, factors such as dispersal strategy (Thomas 2000; Johst et al. 2002) or habitat quality (Matter & Roland 2002) may override the effect of distance. However, our results clearly show that source area distance is important for the millipede assemblages, perhaps because of their limited powers of dispersal (Hopkin & Read 1992; Hamer & Slotow 2002).

These results may apply to many of the other forest taxa and call for careful planning during any restoration program that relies on natural colonization processes. Clearly, if a regenerating community tends to more closely resemble that of the closest source area, both the actual presence of a source area and the community structure there will be crucial in determining the eventual community composition on the regenerating site. If the species pool of the closest source area is small, the likelihood of restoration success decreases and costly management and relocation options may be required. Moreover, this critical dependency on distance to source area is even more important in the case of rare and localized species (Hamer & Slotow 2002), such as is probably the case with the five forest species that have not yet been recorded in any of the regenerating sites, even after up to 54 years of community development.

In summary, from a conservation point of view, our results suggest that anthropogenic disturbances to natural communities may be compensated for by ecological rehabilitation. However, our results also underline the importance of protection from further disturbance, of monitoring changes in regenerating communities over time, and of the need for carefully designed studies to determine for instance why some species colonize, whereas others do not.

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