

COMMUNITY CONVERGENCE IN DISTURBED SUBTROPICAL DUNE FORESTS

T. D. WASSENAAR,^{1,3} R. J. VAN AARDE,¹ S. L. PIMM,^{1,2} AND S. M. FERREIRA¹

¹*Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa*

²*Nicholas School of the Environment and Earth Sciences, Duke University, Durham, North Carolina 22078 USA*

Abstract. Do communities return to their former state when we disturb them? The answer is “surely not always,” since some disturbances may be so devastating that recovery will be impossible. If communities do recover, then how fast is that recovery? Do different subsets of species return at the same rate? Is that rate a simple exponential recovery—meaning that the change toward the original state is fastest when the community is furthest away and it slows as the community converges? Or is recovery a more dynamically complex process? These questions are theoretically interesting and practically important. The theoretical questions are if there is a particular state—some exact composition—to which a community is likely to return, if there might be several (or many) possible such states, or if community composition is essentially haphazard. The practical implication is that if disturbed ecological communities do not tend to return to a previous state, it may be impossible to undo human impacts on natural ecosystems.

We follow the fate of species assemblages following the removal of vegetation for mining. We show that these assemblages in restored subtropical coastal dune forests in South Africa do converge with a regional equilibrium state and that convergence is possible within a reasonable period. However, changes in assemblages from different trophic levels were idiosyncratic: convergence in the dung beetle assemblage did not mimic convergence for trees and birds, for example. Few of the assemblages converged exponentially, the simplest shape for the decay function. Furthermore, trends were sometimes different for different indices of community dissimilarity, suggesting that whether one accepts convergence depends, in part, on exactly what one measures.

Key words: *coastal dune forests, South Africa; community organization; convergence; ecological restoration; mining; resilience.*

INTRODUCTION

Do communities return to their former state when we disturb them, and if they do, how fast is that recovery? Is the rate of recovery in one group of species similar to others? Is the change towards the original state fastest when the community is furthest away and slower as it converges, as it would be if differences from the final community state decayed exponentially? Or is recovery more dynamically complex than such a simple exponential return? Herein, we attempt to answer these questions for a coastal dune forest cleared by mining operations in coastal South Africa.

These questions are practically important. If disturbed ecological communities do not tend to return to a previous state, it may be impossible to undo human impacts on natural ecosystems. No doubt, the most effective way of saving ecosystems threatened by human actions is to conserve them. However, restoration, not conservation, is the only option across tens of millions

of square kilometers of already damaged natural ecosystems (Pimm 2001).

These questions are also theoretically challenging. The question “what is an ecological community” has long been a central theme in ecology. Is there a “climax community,” a particular state involving some exact species composition, to which a community is likely to return? Might there be several (or many) such possible states, or is community composition essentially haphazard? Put in other words, is community composition persistent or fleeting?

The idea of a climax community has a long and controversial history in ecology, one that has not been resolved completely. (See, for example, Clements 1928, Gleason 1939, Horn 1974, Hubbell 1979, Christensen and Peet 1984 and references therein, Condit et al. 1992, Terborgh et al. 1996, Wilson et al. 1996, Phillips et al. 1997, Sheil 1997, Wilson et al. 2000) We know that species composition is seldom constant in natural communities (Sprugel 1991, Inouye 1995) and is often dependent on stochastic changes across various scales of space and time in factors such as climate (Tilman 1987, Sprugel 1991, Davis et al. 2000, Ford et al. 2000). Such changes, however, do not deny the

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³ E-mail: tdwassenaar@zoology.up.ac.za

existence of some state towards which a community will tend to return.

Theoretically, there are numerous possibilities. There can be more than one persistent state, perhaps many more (Drake 1990). The invasion sequence determines the persistent state obtained (Pimm 1991, Lockwood et al. 1997). Theory also suggests a "Hump-ty-Dumpty" effect: it may be impossible to re-assemble a community from its constituent species (Pimm 1991, Drake et al. 1993, Law and Morton 1996, Luh and Pimm 1993). Present day communities may have obtained their present states through an assembly that necessarily included species no longer present. The practical significance of these speculations is that it may be statistically unusual to find a community returning to its original state following disturbance. The frequent failure of ecological restorations to restore desired species composition over ecological time scales (Palmer et al. 1997, Lockwood and Pimm 1999, Stan- turf et al. 2001) is evidence in favor of such a view.

Conversely, there are a number of factors that constrain what a persistent community state might be. The dependence of local communities on regional processes (Cornell and Lawton 1992, Blackburn and Gaston 2001) implies that only a small number of species combinations are possible. Local communities are seldom completely random draws from a regional species pool (Law 1999). Rather they depend on large-scale factors such as species' geographic range size or abundance (Maurer 1999, Blackburn and Gaston 2001). In short, nature constrains the sequence of species recolonizing a disturbed community in ways that models do not.

Recognizing a persistent state is not trivial (Connell and Sousa 1983). A direct way is to determine if the community tends to return to its former composition if the species mix is altered (Hubbell and Foster 1986, Wilson et al. 1996). Terborgh et al. (1996) used such a directional development of tree assemblages on a chronosequence of tropical rain forest sites towards an undisturbed benchmark site as evidence for the operation of biological mechanisms and the existence of a persistent state. Here we use a similar direct approach by following the fate of species assemblages after the removal of vegetation for mining. We evaluate the trajectories of species assemblages from different trophic levels and one set of abiotic factors, relative to a benchmark undisturbed forest in the region. Initially different biological communities converge if there is a shift in composition of the one community (the regenerating community) towards another (the undisturbed benchmark) in the identity or the relative abundances of their constituent species over time (Grover and Lawton 1994). We therefore expect a decrease in some multivariate dissimilarity index (d), based on species composition or species abundance, between benchmark sites and regenerating sites with increasing time since initial disturbance.

The rate of change in community composition is unlikely to be similar near and far away from a stable equilibrium (Ludwig et al. 1997). For resilient, disturbed systems that are reasonably close to a persistent community state (i.e., still within that state's domain of attraction), the simplest trajectory is an exponential decay of d (Pimm 1991). More complex dynamics are possible, of course, and we use the exponential decay in d over time only as a reference.

METHODS

Study area

We studied two separate locations at the southern end of the Maputaland–Pondoland regional center of plant diversity (van Wyk 1996). In one location, we surveyed regenerating coastal dune forest sites (the Tisand lease area of Richards Bay Minerals, abbreviated as RBM), northeast of Richards Bay, KwaZulu–Natal, South Africa. Coastal sand dunes here have been mined for ilmenite, iron, and rutile since 1976 (van Aarde et al. 1996b). The dredge-mining process removes all vegetation and topsoil ahead of the dredge pond. Mining is followed by a rehabilitation process during which reshaped sand tailings are covered with pre-mining harvested topsoil, revegetated with a cover crop of annuals and grasses, and then left to regenerate naturally (van Aarde et al. 1996b). Post-rehabilitation management is limited to the removal of alien vegetation and reseeded of die-offs in the first two years.

The rehabilitation process has created a series of known-aged regenerating areas. They are arranged in a narrow strip on the second and third dune ranges from the coast from Nhlabane in the northwest to ~10 km northeast of Richards Bay (Fig. 1). They do not exceed more than 2 km in width at any point along the coast and are bordered variously by bare sandy mining areas, unmined forest, commercial plantations of beefwood (*Casuarina equisetifolia*), rural dwellings and crops, as well as highly disturbed and scrubby areas dominated by exotic invasive plants. The adjacent unmined forest patches consist of a ~200 m wide strip on the seaward side of the rehabilitating areas as well as a number of small (<1 ha) patches scattered around the mining area.

We used a second location (Sokhulu), an unmined coastal dune forest situated about 20 km northeast of the rehabilitating sites, as a benchmark (Fig. 1). Sokhulu is ~500 ha in size and is contiguous with the Mapelane Coastal Dune Forest Nature Reserve (~1500 ha). Aerial photographs show that the Mapelane–Sokhulu forest patch has been intact since before 1937. The Sokhulu forest patch is typical of coastal dune forests in the region and is the closest relatively large patch of undisturbed forest to the mining lease area.

Mentis and Ellery (1994) and Van Aarde et al. (1996b) described the abiotic (topography, climate, and soils) and biotic (vegetation) characteristics of both

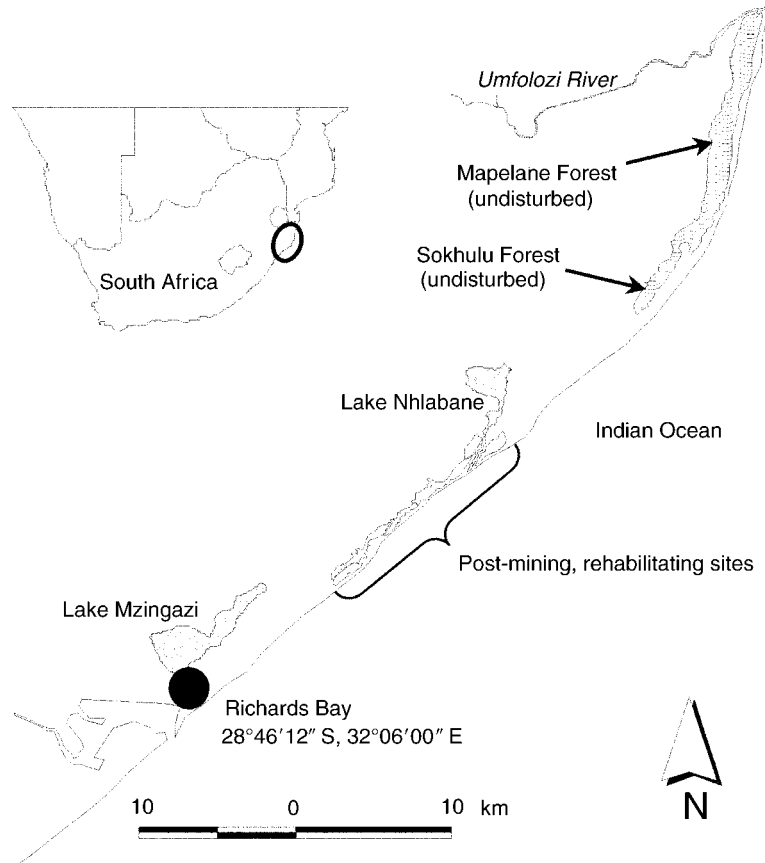


FIG. 1. Map of the study area. The study site (the postmining regenerating areas) is located on the coast about 10 km northeast of the town of Richards Bay, South Africa. Sokhulu is an undisturbed forest used as benchmark for our study and is contiguous with the Mapelane Coastal Dune Forest Nature Reserve to the northeast. Rehabilitating areas are 1–22 years post-mining.

mined and unmined areas. Here, we provide descriptions of only the most salient aspects of the vegetation physiognomy on our study site. In the early stages, the rehabilitating sites are essentially scrubby grasslands dominated by weedy annuals, several grass species, and seedlings of the pioneer tree, *Acacia kosiensis*. By about four years, *A. kosiensis* forms a dense, monoculture stand ~3 m high with very little undergrowth (typically <30% ground cover). Over the next 16–18 years, *A. kosiensis* continues to dominate while it increases in height to ~12 m. By 12 years, a number of other old-forest tree species have started to colonize and a dense undergrowth, consisting mainly of stoloniferous grasses, climbers, and scandent plants, develops. Vegetation cover on the forest floor is then >100% but a true subcanopy layer is still absent. At the time of our last surveys, the oldest sites were ~22 years old and were still dominated by ~15 m high *A. kosiensis*. A subcanopy layer consisting of emerging 2–4 m high forest tree species and lianas is also beginning to appear in places.

The Sokhulu forest site is an undisturbed moist subtropical coastal dune forest (12 to >15 m) with rela-

tively high tree diversity. Dominant tree species are *Celtis africana*, *Mimusops caffra*, and *Ziziphus mucronata*. The undergrowth is patchy and of varying height (10 cm–2 m) and there is a true subcanopy layer consisting of specialist shade-adapted species such as *Psychotria capensis* and *Dracaena alectrifomis*, as well as several lianas (e.g., *Cyphostemma* sp.) and erect woody forbs (e.g., *Isoglossa woodii*).

Data collection

We collated data from published and unpublished sources for six biological assemblages (from the decomposer, primary producer, and consumer trophic levels) and one abiotic group that have all been studied on the site. Details on the methods employed in surveying some of the assemblages and abiotic variables can be found in the following publications: soil, van Aarde et al. (1998); dung beetles, Davis et al. (2003); millipedes, van Aarde et al. (1996a); trees, Theron (2001); small mammals, Ferreira and van Aarde (2000); and birds, Kritzing and van Aarde (1998).

Soil elements.—Soil was sampled using a 1000 cm³ square soil corer. Samples were taken from the upper

TABLE 1. The number of replicates per year per area for each group.

Year	Soil		Herbs		Trees	
	Rehab	Sokhulu	Rehab	Sokhulu	Rehab	Sokhulu
1991						
1992						
1993						
1994			10 (×3)	4		
1995	4–5 (×4)	5	10 (×5)	10		
1996						
1997						
1998						
1999			10 (×6)	25	40–70 (×3)	40
2000						
2001					10–40 (×7)	

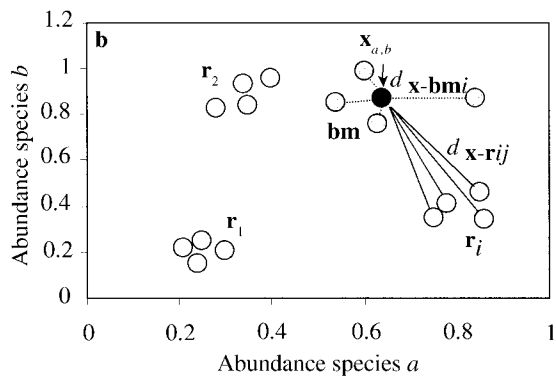
Notes: Numbers in parentheses refer to the number of rehabilitating areas that existed for that year. A new area is rehabilitated about once every three years; thus in 1991 there were only four rehabilitation sites, increasing to eight by 2000. ‘‘Rehab’’ is the collective term for the rehabilitation areas and ‘‘Sokhulu’’ is the benchmark area. For instance, in 1998 four transects were surveyed for birds in each of the six rehabilitating areas that existed at that stage, and eight transects were surveyed in Sokhulu. This resulted in a total of 32 transects for birds in 1998.

10 cm of the soil profile in five randomly located points per site (Table 1). Each sample consisted of six core subsamples that were later mixed together and subsampled for the chemical analyses. In our analysis, we

chose the variables of pH, % carbon, and concentrations of the minerals P, Ca, Mg, K, and Na.

Millipedes.—Millipedes were sampled in randomly located 6 × 35 m transects per site (Table 1). For the

a	Sites																		
	Disturbed (mined and rehabilitated)									Undisturbed									
	Regenerating area 1			Regenerating area 2			...	Regenerating area <i>i</i>			Benchmark			Reference vector					
Species	r_{11}	r_{12}	...	r_{1j}	r_{21}	r_{22}	...	r_{2j}	...	r_{i1}	r_{i2}	...	r_{ij}	bm_1	bm_2	...	bm_j	δ	\mathbf{x}
Species <i>a</i>	a_{11}	a_{12}	...	a_{1j}	a_{21}	a_{22}	...	a_{2j}	...	a_{i1}	a_{i2}	...	a_{ij}	a_1	a_2	...	a_j	-	μ_A
Species <i>b</i>	b_{11}	b_{12}	...	b_{1j}	b_{21}	b_{22}	...	b_{2j}	...	b_{i1}	b_{i2}	...	b_{ij}	b_1	b_2	...	b_j	-	μ_B
...	-	...
Species <i>z</i>	z_{11}	z_{12}	...	z_{1j}	z_{21}	z_{22}	...	z_{2j}	...	z_{i1}	z_{i2}	...	z_{ij}	z_1	z_2	...	z_j	-	μ_Z
Multivariate distance (<i>d</i>)	d_{x-r11}	d_{x-r12}	...	d_{x-r1j}	d_{x-r21}	d_{x-r23}	...	d_{x-r2j}	...	d_{x-ri1}	d_{x-ri2}	...	d_{x-rij}	d_{x-bm1}	d_{x-bm2}	...	d_{x-bmj}	$\mu_{d_{x-bmj}}$	$d_{x-x} = 0$



$$\text{Euclidean distance (ED) is shown by } d = \sqrt{\sum_{k=1}^z (y_{1k} - y_{2k})^2},$$

where y_{1k} is the proportional abundance of the k th species in site 1, and z is the number of species in both sites.

FIG. 2. A graphical summary of data structure and calculation of Euclidean distance. (a) Proportional species abundances were tabulated per site for the mined regenerating areas ($a \dots z_{ij}$) and the undisturbed benchmark area ($a \dots z_j$). The reference vector (\mathbf{x}) is the mean proportional abundance of each species in the undisturbed benchmark. Dissimilarity (d) was calculated as the multivariate distance between the reference vector \mathbf{x} and each sample site. The target is represented by δ , the mean of the group of distances $d_{x-bm1 \dots j}$ between the benchmark sites and \mathbf{x} . (b) The multivariate distance measure ‘‘Euclidean distance’’ is the distance between two points on the two-dimensional plane defined by the proportional abundance of species a and b in each site. Replicate sites within a regenerating or benchmark area appear as clusters ($\mathbf{r}_1, \mathbf{r}_2 \dots \mathbf{r}_i, \mathbf{bm}$). The mean distance between any regenerating area and the reference vector (the solid lines d_{x-rij} connecting each replicate regenerating site with the centroid $\mathbf{x}_{a,b}$) should over time decrease to become, on average, equal to the distance between the benchmark replicates and the reference vector (the dotted lines d_{x-bm} , connecting each replicate benchmark site with the centroid).

TABLE 1. Extended.

Millipedes		Dung beetles		Birds		Mammals	
Rehab	Sokhulu	Rehab	Sokhulu	Rehab	Sokhulu	Rehab	Sokhulu
						1-2 (×4)	2
						1 (×4)	1
				3 (×5)		1 (×5)	1
5 (×4)						6 (×5)	
5 (×5)	5					6 (×5)	3
6 (×5)	6					3 (×5)	2
6 (×5)	6			2-4 (×6)	2	3 (×6)	3
				4 (×6)	8		
6 (×6)	6			3-4 (×6)	4	3 (×6)	3
6 (×7)	6	3 (×8)	6	3-4 (×6)	4	3 (×6)	3

current analysis, only data collected during the spring and summer were used. Three to four observers searched the transect from one side to the next and recorded all millipedes seen up to a height of 3 m. We calculated abundance as the number of individuals per species per transect as a proportion of the total number of individuals per transect.

Beetles.—Eight rehabilitating sites and one benchmark site were surveyed for dung beetles during 2000. Pitfall traps (in three groups of five traps per sampling site) using pig dung as bait were randomly located in the different sites (Table 1). Trapping was conducted over two days during the midsummer seasonal activity peak. We calculated abundance as the number of individuals per species per trapping grid as a proportion of the total number of individuals per grid.

TABLE 2. A graphical representation of how the dissimilarity measure Ochiai's distance is calculated.

Species	Site r_{ij} / \mathbf{bm}_j	\mathbf{x}	
<i>a</i>	1	0	Species unique to r_{ij} / \mathbf{bm}_j (<i>b</i>)
<i>b</i>	1	0	
<i>c</i>	1	1	Shared species (<i>a</i>)
<i>d</i>	1	1	
<i>e</i>	1	1	Species unique to \mathbf{x} (<i>c</i>)
<i>f</i>	0	1	
<i>g</i>	1	0	
<i>h</i>	0	0	
<i>i</i>	0	1	
<i>j</i>	1	0	
<i>k</i>	1	0	
<i>l</i>	0	1	
<i>m</i>	0	1	

Notes: Only species presence (bold 1's) is used. Ochiai's distance is the geometric mean of the ratio of the number of shared species (shaded gray) to the total number of species in both sites. Ochiai's distance (OD) is shown by

$$d = 1 - \frac{a}{\sqrt{(a + b)(a + c)}}$$

where *a* is the number of shared species between two sites and *b* and *c* are the number of species unique to the respective sites.

Herbs.—Forest floor herbaceous vegetation (<1 m) was surveyed in 1994, 1995, and 1999. The number of sampling plots in the rehabilitating sites was the same in all survey years but differed between years in the benchmark site (Table 1). Sampling plots were randomly located per site and consisted of ten 1-m² quadrats laid out in a 2 × 5 pattern with 5 m between each quadrat. Quadrats were subdivided into ten subquadrats (1995 and 1999), and species present recorded per quadrat (1994) and per subquadrat (1995, 1999). We calculated abundance as the number of quadrats (1994) or the number of subquadrats (1995, 1999) per plot per species as a proportion of the total number of quadrats or subquadrats per species per plot.

Trees.—Self-supporting woody plants taller than shoulder height (~1.7 m) were counted during 1999 and 2001 in 16 × 16 m randomly located quadrats (Table 1). Abundance was calculated as the number of rooted individuals per species per quadrat as a proportion of the total number of individuals per quadrat.

Birds.—Line transects (different numbers of transects per year and per site, Table 1) were used to survey birds in 1993 and from 1997 to 2000. Transects were randomly located per site and were separated by at least 200 m. Each transect was walked until at least thirty individuals were observed. We calculated abundance as number of individuals per species per transect as a proportion of the total number of individuals per transect.

Small mammals.—Small mammals (rodents and shrews) were surveyed using Sherman live traps in permanent trapping grids. The numbers of grids per stand varied between years (Table 1). Abundance was calculated as the minimum number of animals alive on the grid per species as a proportion of the total number in the grid.

DATA ANALYSIS

Calculating site age

Rehabilitation date was not recorded at a fine enough resolution to allow an age to be assigned to each sampling unit. We therefore divided the existing rehabili-

TABLE 3. Results of an analysis of post-disturbance changes in species composition and species presence of six assemblages and one functional group (soil), as measured by Euclidean distance (ED) and Ochiai's distance (OD), respectively.

Group	Distance index	Convergence regression		
		Log-linear model	F	df
Soil	ED	$d_t = -0.81 - 0.08t$	26.61	1, 17
Herbs	ED	$d_t = -0.67 - 0.01t$	15.31	1, 108
	OD	$d_t = -0.06 - 0.01t$	200.5	1, 108
Trees	ED	$d_t = 0.28 - 0.04t$	145.4	1, 172
	OD	$d_t = -0.02 - 0.01t$	124.4	1, 172
Dung beetles	ED	$d_t = -0.89 - 0.002t$	0.03	1, 22
	OD	$d_t = -0.30 - 0.02t$	51.56	1, 22
Millipedes	ED	$d_t = -0.47 - 0.03t$	19.97	1, 138
	OD	$d_t = -0.12 - 0.02t$	47.51	1, 138
Small mammals	ED	$d_t = -0.35 - 0.01t$	13.22	1, 106
	OD	$d_t = -0.36 + 0.004t$	1.00	1, 106
Birds	ED	$d_t = -0.48 - 0.04t$	91.61	1, 77
	OD	$d_t = -0.07 - 0.01t$	180.4	1, 77

Notes: Ochiai's distance (OD) was not measured in soil. After disturbance, the \log_e of distance should decay linearly as the new assemblage changes to become progressively more similar to a benchmark undisturbed community. Here we present the results of a least-squares linear regression on \log_e OD and \log_e ED, and an F test for slope significance (significant values are in bold). Years to converge is the number of years, as predicted from the regression, that a disturbed community will take to become as similar to an average benchmark community as replicate benchmark sites are themselves. This value is followed, in parentheses, by the shortest and longest predicted convergence time, calculated as the 95% confidence limits for the predicted site age where convergence occurs. The lack-of-fit test tests for linearity in the relationship between \log_e distance and site age. F values for groups where the relationship is significantly different from linear are in bold.

tation areas by grouping areas that were rehabilitated over a period of up to four years together as a "site," using breaks in the rehabilitation process as guide. We used the median of these rehabilitation years as the starting date from which the site's age was calculated, and added the number of intervening years between the first and each subsequent survey. Each survey was deemed an independent sample representing the composition of the community at a particular habitat age.

Calculating dissimilarity and defining the benchmark using Euclidean distances

The data for one survey consist of the proportional abundances of all the species ($a, b \dots z$) at each of several sites (Fig. 2a). One set of sites was disturbed (mined) at different times in the past, resulting in regenerating sites of different ages ($r_1, r_2 \dots r_i$), while another site, the "benchmark" (**bm**), was undisturbed (Fig. 2a). In each site, we surveyed the plants and an-

FIG. 3. A graphical representation of the relationship between dissimilarity and site age. Multivariate distance (d), calculated as Euclidean and Ochiai's distance between regenerating sites of different ages (the open diamonds) and the reference vector \mathbf{x} , should decay exponentially (solid line) with site age until it approaches δ , which is the mean distance between the benchmark sites (gray diamonds) and \mathbf{x} , and which is here represented by a dotted line. The centroid of \mathbf{x} (where $d = 0$) is represented by the solid diamond $d_{\mathbf{x}\mathbf{x}}$.

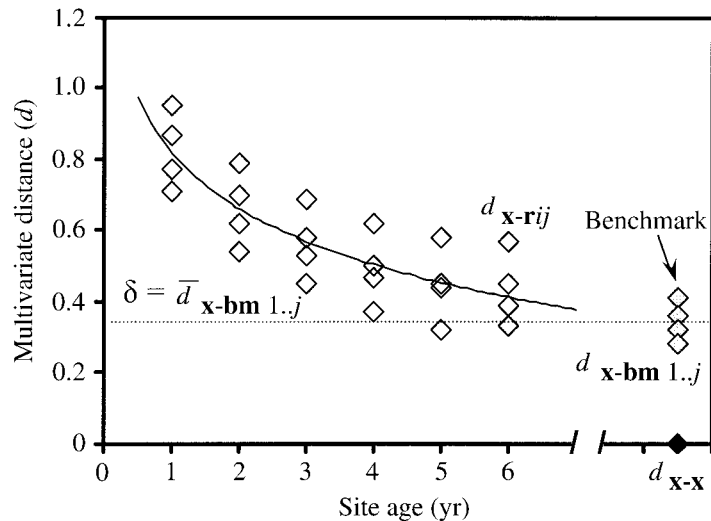


TABLE 3. Extended.

Convergence regression		Lack-of-fit test		
<i>P</i>	Years to converge	<i>F</i>	df	<i>P</i>
<0.001	25.4 (18.3, 38.1)	7.85	2, 15	0.005
<0.001	105.0 (64.0, 211.2)	4.15	6, 102	<0.001
<0.001	32.9 (24.2, 42.5)	2.49	6, 102	0.03
<0.001	38.7 (19.4, 55.3)	18.83	8, 170	<0.001
<0.001	40.5 (25.8, 55.5)	13.54	8, 170	<0.001
0.86	no convergence	12.57	5, 17	<0.001
<0.001	26.8 (16.1, 40.7)	2.32	5, 17	0.09
<0.001	21.6 (-6.7, 54.7)	2.39	14, 124	0.006
<0.001	14.3 (4.3, 41.7)	2.99	14, 124	<0.001
<0.001	24.5 (-7.3, 67.5)	1.24	17, 89	0.25
0.32	no convergence	2.47	17, 89	0.003
<0.001	32.4 (21.4, 44.7)	1.71	16, 61	0.07
<0.001	37.6 (29.4, 46.6)	0.38	16, 61	0.98

imals in several sampling plots or transects ($\mathbf{r}_{11}, \mathbf{r}_{12} \dots \mathbf{r}_{ij}, \mathbf{bm}_1, \mathbf{bm}_2 \dots \mathbf{bm}_j$) (Fig. 2a).

We created a “reference vector” (\mathbf{x}) by taking the mean benchmark proportional abundance for each species (Fig. 2a). The dissimilarity of the different benchmark samples to this reference vector then defines a range of “natural” states (i.e., the natural variability in species composition across a variety of different sites) around the reference vector.

The expectation is that the species composition of the regenerating sites will be much less similar to the reference vector than what the different benchmark sites will be, but their dissimilarity will decrease over time as benchmark species colonize these new habitats. To evaluate the relative dissimilarity of the sites to the reference vector, we calculated the “distance” between each regenerating sample and the reference vector ($d_{\mathbf{x}-\mathbf{r}11} \dots d_{\mathbf{x}-\mathbf{r}21} \dots d_{\mathbf{x}-\mathbf{r}ij}$), as well as between each benchmark sample and the reference vector ($d_{\mathbf{x}-\mathbf{bm}1} \dots d_{\mathbf{x}-\mathbf{bm}j}$) (Fig. 2a). Finally, we calculated $\mu_{d_{\mathbf{x}-\mathbf{bm}1} \dots j}$, which is the mean of the distances between the benchmark samples and the reference vector and is also our target value δ (Fig. 2a). Quite what we mean by “distance,” we shall explain in the following paragraph.

To illustrate the calculation of the multivariate distance measure, in this case Euclidean distance, we can represent these data as a two-species simplification, plotting the proportional abundance of species b vs. species a (Fig. 2b). In this two-dimensional example, Euclidean distance is the simple linear distance, in units of proportional abundance, between any two points on this plane. For our data, the several replicate plots for each site age appear as a cluster of points in the graph (\mathbf{r}_1 is a site-age cluster, as is \mathbf{r}_2 ; \mathbf{r}_i is a cluster, etc.) (Fig. 2b). The benchmark samples also form a cluster around the centroid $\mathbf{x}_{a,b}$, which is the reference vector represented as a point in two-dimensional space in Fig. 2b. The mean proportional abundances of this two-

species community on a regenerating area should change over time to become more similar to the mean proportional abundances on the benchmark area. Hence, the distances between each replicate site on a regenerating area and the reference vector $\mathbf{x}_{a,b}$ (solid lines, $d_{\mathbf{x}-\mathbf{r}ij}$) should decrease, until it is, on average, equal to the distances between the benchmark replicates and the reference vector (dotted lines, $d_{\mathbf{x}-\mathbf{bm}j}$) (Fig. 2b). The two-dimensional distance from our example is easily extended to a multi-dimensional space defined by the proportional abundances of all species in all the sites through the equation for Euclidean distance (ED): $d = \sqrt{\sum_{i=1}^z (y_{1k} - y_{2k})^2}$, where y_{1k} is the proportional abundance of the k th species in site 1, and z is the number of species in both sites (see also Fig. 2b).

Calculating dissimilarity and defining the benchmark using Ochiai’s distance

“Distance” can also be measured in a number of other ways. Euclidean distance will mostly be affected by differences in species proportional abundances and will be relatively insensitive to local colonizations and extinctions unless such species have high proportional abundances. However, communities can also change over time due only to species turnover, independently of finer changes in relative abundances. In such a case, two sites sharing many species (the species in the shaded region of Table 2), relative to the number of species unique to each site, will be more similar to each other than two that share few species. We therefore calculated an alternative distance measure, Ochiai’s distance (OD) (Legendre and Legendre 1998), which is the geometric mean of the ratios of the number of shared species to the total number of species in each site: $d = 1 - a/\sqrt{(a+b)(a+c)}$, where a is the number of shared species between two sites, and b and c are the number of species unique to the respective sites (see also Table 2). Ochiai’s distance is sensitive only to species pres-

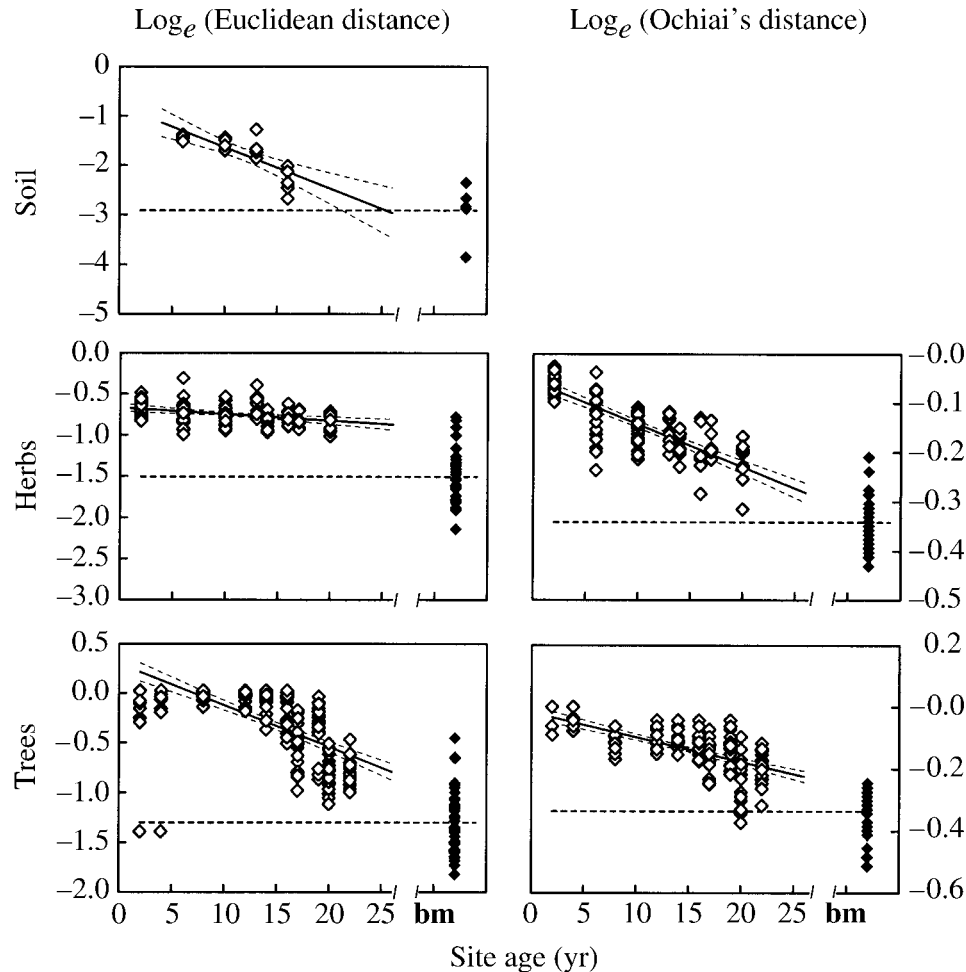


FIG. 4. The change in assemblages of herbs, trees, millipedes, dung beetles, small mammals, and birds, as well as a group of soil elements (pH and a variety of minerals), after disturbance (mining) and subsequent rehabilitation of coastal dune forests, compared to the same assemblages on an undisturbed area. Here we regress (solid lines, with dotted 95% CL) the natural logs of two dissimilarity indices: Euclidean distance (on the left [on this page and on the facing page]), which is sensitive to species relative abundances, and Ochiai's distance (on the right), which is sensitive only to species presence, on site age. The solid diamonds on the right in each graph, which are not of any particular age, represent the variability in either species relative abundance (Euclidean distance), or composition (Ochiai's distance) on the undisturbed benchmark (**bm**) area. The mean of these, the dotted horizontal line in each graph, is the target value at which the regenerating area will become as similar to the average benchmark assemblage as the benchmark is itself. Ochiai's distance was not used for the soil group.

ence and absence and was therefore not appropriate for the soil elements.

Model of multivariate distance decay

In Fig. 3, we show the hypothetical relationship between the distances calculated above (using either of the two methods), and the age of the site. At the right are the distances between the benchmark samples and the reference vector (gray diamonds). The mean of these, our target value δ , is represented by a horizontal dotted line. At the left (open diamonds), we show the distances for each site plotted against the age in years of the site. The reference vector has, trivially, a distance

d_{xx} of zero to itself (the solid diamond in the lower right of Fig. 3).

In this hypothetical example, convergence is an exponential decay described by the equation $d_t = d_0 e^{(-kt)}$, where d_t is the distance index after t years since disturbance, d_0 its initial value, and k is a rate constant that measures resilience (Pimm 1991, 1999) (Fig. 3). Convergence is complete when the samples from a regenerating site are, on average, as different from the reference vector as are the benchmark samples.

Were the distances indeed decaying exponentially, then the logs of the distances would decay linearly as the age of the site increases. The test for convergence

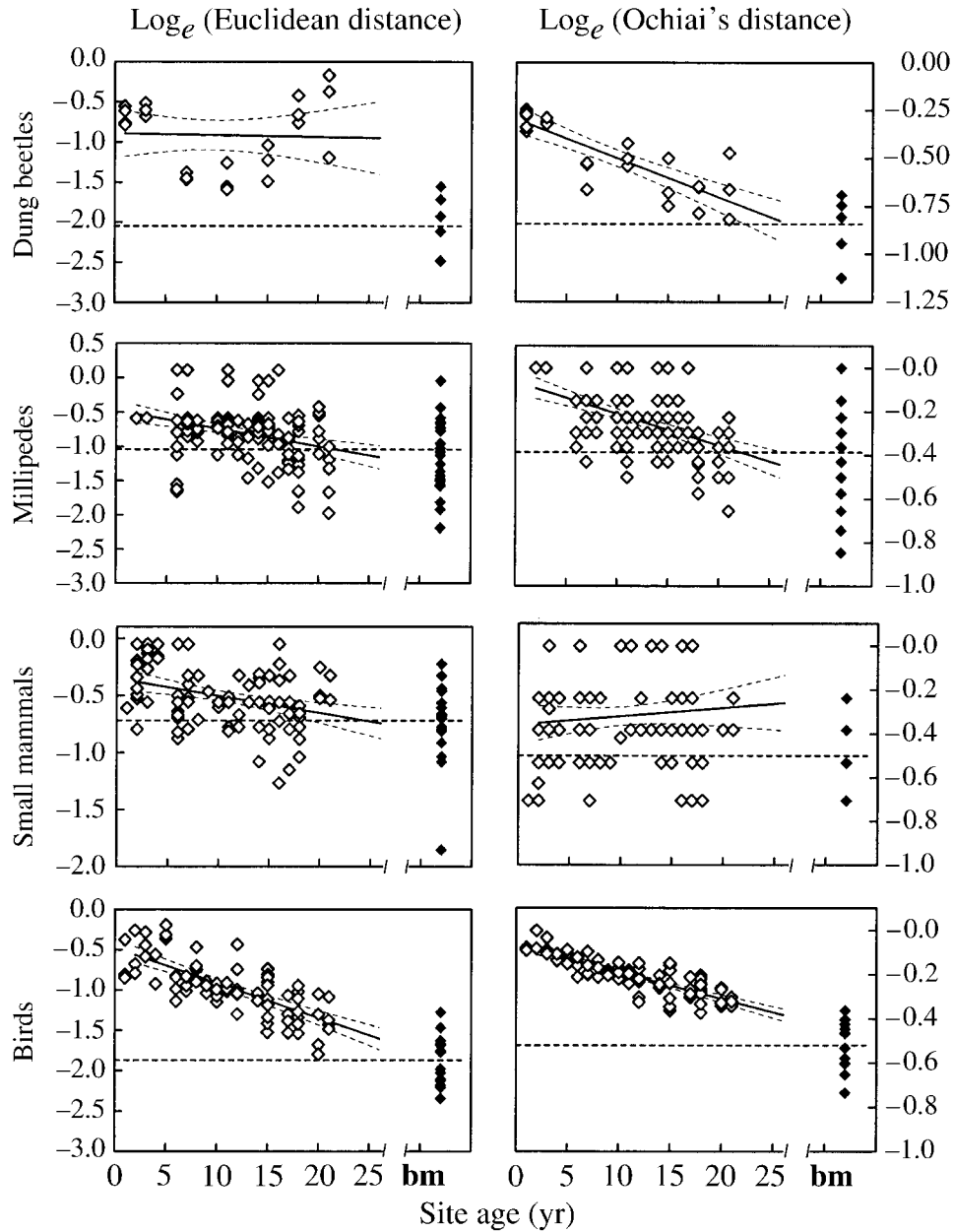


FIG. 4. Continued.

is that the slope of the log-linear regression line is significantly less than zero. Furthermore, if the relationship between log distances and site age is linear, then convergence is exponential. Since there are multiple observations for each site age, we test for linearity by partitioning the residual variance about the linear regression into within-age variance (“pure error”) and the remaining lack of fit variance. If the latter is sufficiently large (as measured by an *F* test), we reject the linear decline in log distance.

To estimate the approximate time it will take to complete convergence we used the regression model

to calculate the predicted site age at which differences between the rehabilitating sites and the reference vector are, on average, as different as the sites within the benchmark (i.e., where $d = \delta$). We also estimated a minimum and maximum time to convergence by calculating 95% confidence limits for the predicted site age where $d = \delta$ (Sokal and Rohlf 1995). The regression is an empirically fitted line, hence predicted convergence times are uncertain if the true trajectory is not exponential. However, in lieu of a structural model of distance decay, this is the best estimate that we have of the time it will take the different com-

munities to recover a species composition typical of dune forests.

RESULTS

With the exception of the relative species abundances of dung beetles (measured by Euclidean distance, ED) and the species composition of the small mammals (measured by Ochiai's distance, OD), the community abundances and composition converged significantly towards the benchmarks as the time after disturbance increased (Table 3; Fig. 4).

Only one of the cases, the relative abundances (ED) of herbs, was predicted to take longer than 41 years after disturbance to converge (Table 3). Even the upper 95% confidence intervals for the predicted time to convergence (with the exception of the herbs) were less than 68 years (Table 3). Indeed, a number of the groups, including composition (OD) of the soil elements (pH and a variety of minerals), dung beetle species composition (OD), millipedes relative abundance (ED), and small mammal relative abundance (ED) and composition (OD) had already converged, or were about to converge at the time of our study (Table 3). However, confidence intervals (the difference between the upper and lower estimated time to convergence) for some of the groups at least were very wide, being twice (or more) the estimated time to convergence itself (Table 3). Confidence intervals ranged from only 17 years for the birds (OD) to 147 years for herbs (ED) (Table 3).

The relationship between site age and log distance was linear (i.e., convergence was exponential) in only four of the 13 cases: dung beetles species composition (OD), and birds composition (OD) and relative abundance (ED) (Table 3; Fig. 4). Nonexponential convergence is particularly evident in the soil elements (ED), trees (both OD and ED), and dung beetles (ED) (Fig. 4). Both trees and soil elements remained at or near their initial values for between 12 and 15 years before decreasing, while dung beetle relative abundances diverged after the first 15 years of convergence (Fig. 4). Particularly small mammals and millipedes were characterized by a large amount of variability (Fig. 4). Indeed, in the majority of the cases, variability in the benchmark area exceeded that of the regenerating areas, even the oldest ones (Fig. 4). The exceptions were trees and dung beetles, where variability appeared to increase with site age, approaching that of the benchmark in at least the dung beetles (Fig. 4). Overall, the pattern produced by relative abundances (ED) was similar to that of composition (OD) for the herbs, trees, and birds, but very different in dung beetles, millipedes, and small mammals (Fig. 4).

Two outliers at 1 and 4 years post-disturbance in tree relative abundances (ED) actually consisted of six sites that had no trees (Fig. 4). We omitted these data, which were the result of a peculiarity of the Euclidean distance index (see Legendre and Legendre 1998), from the regression analysis.

DISCUSSION

We found that with the exception of two cases, species composition (measured here by Ochiai's distance, OD) and relative abundance (measured with Euclidean distance, ED) became significantly more similar to a reference system as the assemblage's age increases. Moreover, convergence was reasonably fast and the trajectories reasonably constant: with the exception of herbs (ED), all predicted convergence times were less than 41 years on average, and less than 68 years at the maximum. This amounts to no more than a few generations for any of the groups in our study and is less than the lifespan of most of the tree species. Variability in the benchmark was still more than in the oldest regenerating sites for most groups, but in the trees and dung beetles variability appeared to increase with site age (perhaps because of a stochastic element in colonization rates). Overall, our results are not evidence for (or against) any specific community assembly mechanisms, but do suggest that real communities must experience some type of structuring during the assembly process.

Much of the argument around the existence of persistent states, and hence the probability of community recovery, may lie in the ecological detail that models often ignore. For instance, we found a disparity between relative abundance (ED) and species presence (OD) for both small mammals and dung beetles. One community may therefore recover only its species composition, while another may recover both. A persistent state may thus be in the eye of the beholder, and using a distance index that measures only presence or only abundance may lead to a different conclusion. Furthermore, in small mammals (relative abundance or ED) and millipedes (both distance indices) the pattern was variable, leading to wide confidence intervals in the predicted time to convergence. Yet, the rate of convergence was still highly significant. This variability may thus be seen as implying that the occurrence, and relative abundance, of species is random across the age gradient, but it may also be influenced by the sampling technique (live trapping of mobile animals is not nearly as efficient at sampling a community as quadrat sampling of sessile plants). The absence of convergence in small mammal species composition (OD) implies that this assemblage is not returning to a persistent state, but an equivalent variation in the benchmark forest's assemblage suggests that "persistent state" is perhaps a misnomer for small mammals.

If colonization and extinction rates on a new habitat decrease over time as a function of diversity (MacArthur and Wilson 1967, Manne et al. 1998), dissimilarity should also decay exponentially. From our results, it appears that colonization and extinction (and the concomitant change in relative abundances) are anything but the orderly events foreseen by equilibrium biodiversity theory. Only in dung beetles (OD) and

birds (ED and OD) was the decay in dissimilarity exponential. In some of the groups, the rate of decay was apparently either faster (dung beetles) or slower (trees) than exponential in the initial stages. For trees, this may be explained by simple successional dynamics (Finegan 1996), where the presence of a long-lived set of pioneer species will result in a lag period in the decay of dissimilarity. Dung beetle population levels are probably influenced by nonlinear changes in microclimatic variables across the chronosequence (Davis et al. 2003), but external disturbances such as the presence of cattle dung at certain times of the year may play a role.

In at least three of the groups (herbs, trees, and birds), the variability on the regenerating sites was much smaller than on the benchmark. This suggests that the regenerating assemblages have so far managed to assemble only a portion of the possible species combinations present across the range of undisturbed forest. The regenerating sites have converged, on average, but have attained only a portion of the undisturbed forest's beta diversity. Complete convergence here may thus critically depend on colonization by a subset of species that are either simply very rare, or require the presence of dispersal agents (Richardson et al. 2000), or a particular habitat component (such as large old trees for nesting holes).

In conclusion, we have demonstrated that real communities may return to a persistent state within at the most a few generations. Indeed, with only a few exceptions convergence seems to be a common type of post-disturbance change, at least in these dune forests. This has many obvious implications for ecological restoration, which has had mixed results (Lockwood and Pimm 1999). Furthermore, in the debate over whether stabilizing mechanisms, internal to the community or not, exists (Hubbell 1979, 2001, Wilson et al. 1996, Clark and McLachlan 2003), we conclude that there are such mechanisms. In a real regenerating forest community, resilience is a demonstrable fact and the number of possible end states is at best small for various, perhaps even opposing, reasons.

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