

# The bird communities of rehabilitating coastal dunes at Richards Bay, KwaZulu-Natal

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*Expected trends of expanded diversity and numbers of species with a limited distribution as a result of increasing habitat regeneration age were observed for bird communities on a rehabilitating successional sere of coastal dune vegetation in KwaZulu-Natal. Bird density did not increase with regeneration age. An almost complete turnover of species occurred, with the characteristic avifauna changing from grassland species, through shrubland species, to birds typically associated with forest. On the evidence of discriminating bird species, dense undergrowth and large, old trees appear to be responsible for differences between the avian communities of rehabilitating and unmined forests. Changes in the avifauna support theoretical models of succession and are similar to observations made elsewhere.*

The development of bird communities is characterised by increases in density (although often not uniformly<sup>1,2</sup>), biomass,<sup>3</sup> species richness<sup>3,4</sup> and indices of species diversity<sup>1,3</sup> during ecological succession. However, diversity sometimes declines during late successional stages.<sup>5</sup> During succession the environment usually changes from unstable to more stable,<sup>4,6</sup> leading to the hypothesis that generalist species dominate in early successional habitats and are replaced by specialists in more mature habitats.<sup>4,7</sup>

The post-mining rehabilitation of coastal sand dune forest vegetation north of Richards Bay (28°38'S, 32°20'E) in KwaZulu-Natal, South Africa, is characterised by ecological succession.<sup>8</sup> As the same procedure was used to rehabilitate mined dunes for 15 years prior to the present study, the mined area comprised a known-aged sequence of stands of vegetation representative of early stages of a sere of coastal dune forest succession.<sup>8,9</sup> Adjacent, unmined stands are known from aerial photographs to have been 30–35 years old at the time of the study, while relatively undisturbed stands on the seaward side of the rehabilitating dunes were at least 50 years old at the time of the study. The latter stands may be considered representative of later stages of coastal dune forest development.<sup>8</sup>

This paper focuses on age-related trends in total (community) density, diversity and community composition of the avifauna. It aims to describe changes in bird community macro-parameters<sup>10</sup> and community composition over 15 years of coastal dune forest rehabilitation (early stages of succession) and to compare these with those recorded for the avian population of an adjacent unmined coastal dune forest. This is primarily a descriptive paper, although the following hypotheses will be tested:

- Bird species diversity, species richness and density do not increase with habitat regeneration age, and
- relative specialisation of species does not increase with habitat age.

## Materials and methods

*Total density and species-specific relative densities.* Five rehabilitating stands of known age, each spanning approximately three calendar years, and unmined areas older than 35 years at the time

of the study, adjacent to the stands, were studied. Van Aarde *et al.*<sup>8</sup> have described the study sites and Kritzinger<sup>11</sup> described the survey design. The study is based on information obtained using line transect surveys,<sup>12</sup> thus it reflects only bird species for which, through direct observation, a sighting distance could be recorded accurately. This resulted in aerial feeders (swifts and swallows) and birds of prey being excluded from the present analysis. The variables presented here therefore do not refer to all birds occurring in the area.

Three fixed transects of between 425 m and 500 m each were laid out in all of the stands except the youngest, in which only one transect was placed due to its small area. To facilitate movement along the transects, all woody vegetation in a strip <1 m wide along the transects was removed. Each transect was sampled at intervals of one to two months between May 1993 and July 1994. Data were analysed for each survey using the computer program DISTANCE<sup>13</sup> to obtain an estimate of total density (birds per hectare) for that day (consisting of up to seven repeats of a transect, on one day). Due to a lack of independence, data obtained during repeated sampling of the same transect were not treated as replicates. Estimates of species-specific densities took differences in visibility between different species into account. Relative visibility ( $r_v$ ) for all species was estimated from the mean sighting distance ( $r_{Dist}$ ) via a significant regression ( $r_v = r_{Dist} \times 0.044 + 0.28$ ;  $r^2 = 0.62$ , d.f. = 60,  $P < 0.001$ ) obtained from 68 species–stand combinations for which species-specific densities were available.<sup>11</sup>

Yellow Weavers (*Ploceus subaureus*) and Lesser Masked Weavers (*P. intermedius*) could not consistently be distinguished due to the similar appearance of females as well as the formation of large flocks containing both species. In this paper we treat the two species as a single morphospecies. Based on differences in avifauna composition (relative species-specific densities), three sampling periods were identified which extended from May to September 1993, from October 1993 to 15 March 1994, and from 16 March to June 1994, respectively.<sup>11</sup> Data from the three periods were analysed separately as they could conceivably reflect on intra-annual changes in the bird community of the area.

*Species richness and rarefaction.* Species richness ( $S$ ) was recorded as the total number of species observed during a sampling period in a stand. Because the number of sightings influences species richness recorded, rarefaction curves were constructed to calculate the expected number of species in a sample of individuals smaller than the original sample.<sup>14</sup> The expected number of species  $E(S_n)$  in a random sample of  $n$  individuals drawn without replacement from  $N$  individuals was calculated using the equation:

$$E(S_n) = \sum_{l=1}^s 1 - \left[ \frac{\binom{N-n_l}{n}}{\binom{N}{n}} \right]$$

where  $n_l$  = the total number of individuals of species  $l$  and the summation is over all species.<sup>15</sup>

*Species diversity.* Hill's numbers,<sup>16</sup> a family of related diversity indices, were calculated for each occasion on which each transect was surveyed as:

$$N_0 = S, N_1 = e - \sum_{I=1}^{S^*} (p_i \ln p_i) \text{ and } N_2 = 1 / \sum_{I=1}^S p_i^2$$

where  $p_i$  = the relative density of species  $I$ . The three indices can be interpreted to indicate mean number of species ( $N_0$ ), the number of common species ( $N_1$ ) and the number of very common species ( $N_2$ ), respectively.  $N_1$  is related to the Shannon diversity index, whereas  $N_2$  represents Simpson's diversity index. Each transect in a stand was taken as a sample, and the data for different sampling periods were analysed separately. The values for each transect (sample) were then used to obtain a mean for each stand. Age-related trends in diversity and total density were analysed using linear least-squares regression analyses on data from rehabilitating stands only. A Student's  $t$ -test was used to test if the slope of these lines differed significantly from zero.

*Rank-abundance curves.* Rank-abundance curves<sup>17</sup> were constructed by plotting the relative densities of each species (on a logarithmic scale) against the species ranks. Least-squares linear regression analyses of the log-transformed relative densities were used to fit lines and enable the comparison of slopes between different stands, which are indicators of equitability.<sup>17</sup>

*Ordination.* To visualise changes in community composition with stand age, data from the different transects were ordinated by non-metric multidimensional scaling<sup>18</sup> (MDS) of Bray-Curtis distances.<sup>19</sup> Calculated stress values indicate how well the rank

similarity is represented in reduced dimensions, with values  $<0.1$  suggesting a good ordination with little risk of misinterpretation.<sup>20</sup>

*Typical and discriminant species.* The method of Clarke<sup>20</sup> was used to determine the contribution and consistency of contribution of different species to between-stand dissimilarity and similarity (SIMPER analysis<sup>20</sup>). Species that contributed most to differences between the oldest rehabilitating stand and the unmined forest were considered discriminant species, while species that contributed most to within-stand similarity were considered as typical species of each stand.

Fourth-root transformed species-specific relative densities for each transect in the oldest rehabilitating stand and in the unmined forest were used for the identification of discriminant species during October 1993 to 15 March 1994 and 16 March to July 1994. Typical species were identified using the fourth-root transformed species-specific relative densities on each transect and during all three survey periods for each stand.

Changes in the relative densities of species discriminating between the oldest rehabilitating stand and the unmined forest, related to habitat age, were examined and interpreted in terms of information on their natural history. This analysis was conducted only for the October 1993 to 15 March 1994 and 16 March to July 1994 sampling periods, because only one transect was surveyed during May to September 1993.

*Relative turnover rate.* Relative turnover rates were calculated using mean Bray-Curtis distances between consecutive rehabilitating stands. These were rescaled to fall between 0 and 1 by subtracting the mean distance within the unmined forest and multiplying by the mean distance between the youngest

Table 1. Density (birds per hectare), number of species, mean species richness per day ( $N_0$ ) as well as Hill's numbers  $N_1$  and  $N_2$  (diversity) in rehabilitating stands of different ages and an unmined stand during three sampling periods. All means are followed by the standard error of the mean. The number of transects in each stand surveyed at least once during each sampling period is also given.

Sampling period	Age of stand in years	Number of transects	Total density	Number of species	Hill's numbers		
					$N_0$	$N_1$	$N_2$
1 May – 30 September 1993	0–2	1	3.4	14	10.0	4.8	3.7
	3–5	3	7.5±1.1	20	9.3±0.5	4.7±0.3	3.4±0.3
	6–8	3	16.1±15.5	32	14.1±1.3	8.7±0.5	6.7±0.3
	9–12	3	8.4±1.2	42	16.7±1.7	8.5±1.2	5.9±0.7
	13–15	3	8.3±1.0	36	17.3±0.3	9.7±1.2	6.8±1.1
	Unknown <sup>1</sup>	1	15.0	26	21.5	11.3	6.6
1 October – 15 May 1994	0–2	1	6.9	14	7.8	3.4	2.5
	3–5	3	7.3±5.6	18	6.4±0.3	3.4±0.1	2.7±0.1
	6–8	3	12.5±4.0	39	13.3±1.4	8.3±0.7	6.6±0.6
	9–12	3	4.7±3.1	33	10.6±1.5	6.1±0.6	4.6±0.3
	13–15	3	5.3±7.0	32	12.8±1.0	8.1±0.6	6.0±0.5
	Unknown <sup>1</sup>	3	12.7±9.5	47	19.5±1.3	11.6±0.6	7.9±0.8
16 May – 30 July 1994	0–2	1	3.3	13	8.5	4.9	3.9
	3–5	3	16.5±80.2	19	10.7±1.2	5.5±0.8	3.9±0.6
	6–8	3	11.0±1.4	28	15.8±1.3	10.2±1.2	7.8±0.9
	9–12	3	12.9±71.4	31	16.0±1.0	8.3±0.4	5.6±0.6
	13–15	3	10.8±0.1	29	16.5±0.5	9.6±0.6	7.1±0.8
	Unknown <sup>1</sup>	3	26.4±53.2	40	23.3±1.3	16.0±0.7	12.1±1.0

<sup>1</sup>Stand of unmined forest representing a late seral stage of coastal dune forest succession.

Table 2. The slopes of the rank-abundance curves. Slopes are negative, and decrease with stand age. A shallower slope (lower absolute value) is an indication of higher equitability.

Age of stand in years	Slopes of rank-abundance curves		
	1 May – 30 Sept. 1993	1 Oct. – 15 May 1994	16 May – 30 July 1994
0–2	-0.136	-0.171	-0.173
3–5	-0.131	-0.175	-0.132
6–8	-0.079	-0.065	-0.066
9–12	-0.056	-0.086	-0.071
13–15	-0.066	-0.083	-0.071
Unknown <sup>1</sup>	-0.071	-0.052	-0.045

<sup>1</sup> Stand of unmined forest representing a late seral stage of coastal dune forest succession.

rehabilitating stands and unmined forest. Both fourth-root transformed and untransformed relative densities were used in the calculation.

**Weighted distribution coefficient (WDC).** The areal distribution of a species on a map<sup>21</sup> was measured using an image analyser (Quantimet 520 Image Analyser, Cambridge Instruments). The distribution coefficient of a given species was calculated as the area of its southern Africa distribution divided by the maximum area measured for any species. The weighted distribution coefficient for each transect in each sampling period then was calculated by multiplying the distribution coefficient of each species by its relative density on that transect for that period. WDC values were transformed to the natural logarithm and regression analyses were performed to determine age-related trends.

**Results**

**Density and diversity.** Stand-specific total bird densities varied considerably and the increase in values with stand age over the initial eight years of habitat regeneration were followed by variable trends. Densities for the different sampling periods were

higher in the unmined forests than on most of the rehabilitating stands. All measures of diversity increased with stand age, with the highest values recorded in the unmined forest (Table 1).

Expected species richness based on rarefied species–area curves suggests that richness on unmined areas was higher than on rehabilitating stands, except during May to September 1993, when only one unmined transect was sampled. In all cases expected species richness at any number of sightings was lower in rehabilitating stands younger than six years than in older. The slopes of the rank-abundance curves decreased with the age of rehabilitating stands during all three sampling periods, and those for the unmined stand were the shallowest, except during May to September 1993 (Table 2).

The slopes of the regression lines of stand age against density did not differ significantly from zero, thus resulting in our failing to reject the null hypothesis of no increase in density with stand age. For all measures of diversity, however, the null hypothesis of no increase in diversity with regeneration age was rejected, except for  $N_2$  during the sampling period 16 March to 31 July 1994 (Table 3).

**Typical species.** The typical species for each stand as indicated by the SIMPER analysis differed among stands, with Fantailed Cisticola, Tawnyflanked Prinia and weavers (Yellow and Lesser Masked) being typical for the youngest rehabilitating stand (0–2 years old), which consisted of grasslands and some low growing *Acacia karroo* (Table 4). On the 13–15-year-old stand Yellowbreasted Apalis and Bleating Warbler, followed in decreasing order by Puffback, Squaretailed Drongo, Forest Weaver, Cape White-eye, and Blackeyed Bulbul, were the typical species. The last five species commonly occurred in mixed flocks that apparently formed around Squaretailed Drongo and Fork-tailed Drongo. On these stands 2–3-metre-high saplings of a variety of broadleaved forest tree species and shrubs produced a developing middle layer. The undergrowth layer of shrubs and herbs was well developed.

Typical species, in decreasing order, for the unmined stand (dominated by *A. karroo*) were Bleating Warbler, Yellowbellied Bulbul, Yellowbreasted Apalis, Olive Sunbird, Collared

Table 3. Summary of regression analyses for different macro-parameters (defined in text and Table 1) against stand age of rehabilitating stands. Significant *P* values are printed in bold face.

Sampling period	Regression variables	Macro-parameters				
		Density	Number of species	$N_0$	$N_1$	$N_2$
1 May – 30 September 1993	Degrees of freedom	12	12	12	12	12
	Slope of regression ± s.e.m.	0.14±0.33	1.35±0.25	0.76±0.15	0.46±0.12	0.29±0.10
	Coefficient of determination ( $r^2$ )	0.02	0.73	0.71	0.58	0.44
	<i>F</i>	0.18	29.09	26.94	15.34	8.50
	<i>P</i>	0.683	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.002</b>	<b>0.014</b>
1 October – 15 May 1994	Degrees of freedom	12	12	12	12	12
	Slope of regression ± s.e.m.	-0.28±0.27	0.76±0.34	0.48±0.19	0.38±0.12	0.27±0.10
	Coefficient of determination ( $r^2$ )	0.09	0.32	0.37	0.48	0.41
	<i>F</i>	1.08	5.14	6.53	10.12	7.68
	<i>P</i>	0.320	<b>0.044</b>	<b>0.027</b>	<b>0.009</b>	<b>0.018</b>
16 May – 30 July 1994	Degrees of freedom	11	11	11	11	11
	Slope of regression ± s.e.m.	0.08±0.62	0.97±0.22	0.67±0.16	0.39±0.15	0.26±1.13
	Coefficient of determination ( $r^2$ )	0.00	0.66	0.63	0.40	0.28
	<i>F</i>	0.02	19.00	17.13	6.78	3.98
	<i>P</i>	0.90	<b>0.001</b>	<b>0.002</b>	<b>0.026</b>	<b>0.074</b>

Table 4. Typical species and their percentage contribution to mean within-stand similarity in different stands. Typical species for each stand are defined as those contributing most to the mean within-stand similarity. Only those species contributing 50% of the within-stand similarity are listed as the typical species for the stand. 'Weavers' refers to Yellow Weaver and Lesser Masked Weaver, which could not be consistently distinguished from each other.

Age of stand in years	Typical species	Percentage contribution to similarity
0-2	Fantailed Cisticola	26.2
	Tawnyflanked Prinia	17.3
	Weavers	15.2
3-5	Rattling Cisticola	21.8
	Weavers	16.0
	Tawnyflanked Prinia	12.7
6-8	Yellowbreasted Apalis	11.9
	Bleating Warbler	11.5
	Tawnyflanked Prinia	10.3
	Weavers	8.8
	Whitebrowed Robin	8.7
9-12	Yellowbreasted Apalis	14.1
	Bleating Warbler	11.1
	Weavers	10.6
	Cape White-eye	8.0
	Puffback	7.1
	Yellowbreasted Apalis	10.3
13-15	Bleating Warbler	9.5
	Puffback	7.0
	Squaretailed Drongo	6.3
	Forest Weaver	6.2
	Cape White-eye	6.1
	Blackeyed Bulbul	6.1
	Bleating Warbler	7.8
	Yellowbellied Bulbul	6.6
	Yellowbreasted Apalis	6.5
	Olive Sunbird	6.3
	Collared Sunbird	6.3
	Cape White-eye	5.7
Goldenrumped Tinker Barbet	5.4	
Forest Weaver	5.4	
Puffback	5.0	

Sunbirds, Cape White-eye, Goldenrumped Tinker Barbet and Forest Weaver. However, the 12 most typical species for this stand were the same as those for the 13-15-year-old rehabilitating stand, while five of the species contributing 50% to within-stand similarity in each stand are shared between the two stands. Forest and thicket specialists such as the Knysna and Purplecrested Lourie, Narina Trogon, Wattle-eyed Flycatcher and Bluemantled Flycatcher were seen on these stands, whereas 12 species were seen only in the unmined stand.

**Turnover.** The temporal development of the avifauna was characterised by an almost complete turnover of species. Excluding occasional strays (bird species seen on less than two occasions in

at least two stands during the study period), only six species were recorded in all the stands. These were Blackeyed Bulbul, Cape White-eye, weavers (Yellow and Lesser Masked), Yelloweyed Canary and Tawnyflanked Prinia.

Relative turnover rate decreased with habitat age and the turnover rate between the 9-12 and 12-15-year-old stands was only marginally higher (0.02 for fourth-root transformed data and 0.04 for untransformed data) than the zero scaled for the differences between transects on the unmined stands (Fig. 2).

**Interstand differences in community composition.** Figure 1 summarises the results of the multi-dimensional scaling ordination of fourth-root transformed relative density data for the different transects in each of the stands. The trends reflected for all three sampling periods are similar, with intra-stand differences in general being smaller than those between stands, and older rehabilitating stands closer to the unmined forest than younger rehabilitating stands.

The contribution of the different species to the Bray-Curtis distances between the oldest rehabilitating and the unmined stands for October 1993 to 15 March 1994 and 16 March 1994 to

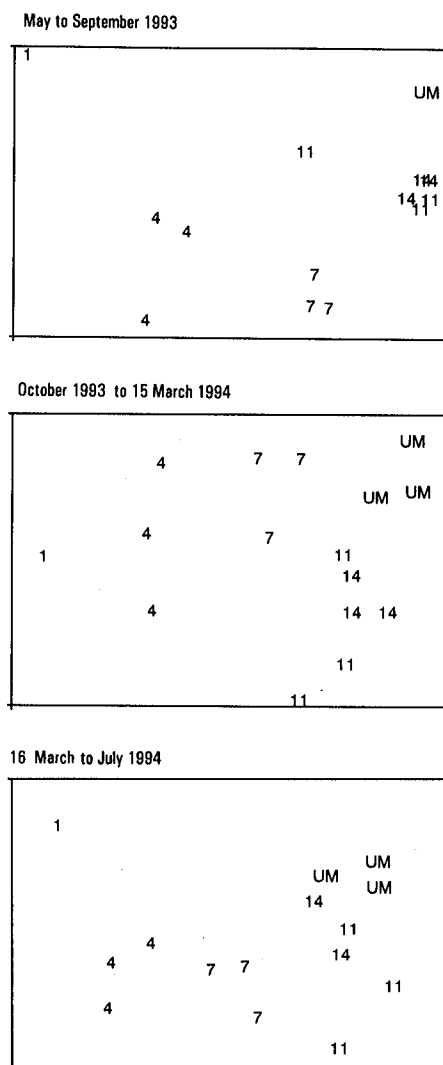


Fig. 1. A non-metric multidimensional scaling (MDS) ordination of the different transects as defined by Bray-Curtis distances calculated from fourth-root-transformed relative densities. Transects are indicated by the median stand age in years; UM refers to the unmined stand. Stress values for the three ordinations are 0.05 for May-September 1993, 0.06 for October 1993-15 March 1994 and 0.10 for 16 March-July 1994.

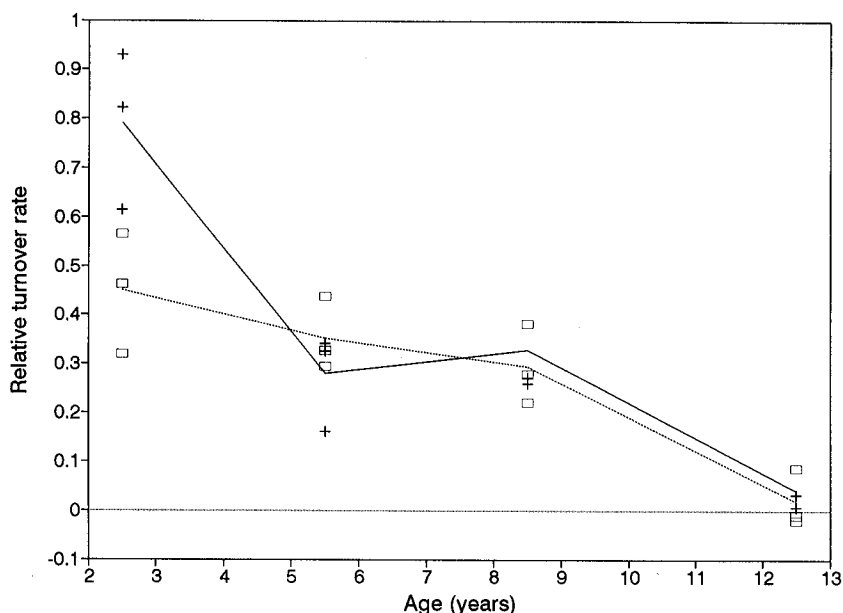


Fig. 2. Change in relative turnover rate with stand age in rehabilitating coastal dune forests. Turnover rate was measured as the Bray-Curtis distance between consecutive stands and is plotted at an age intermediate between the two relevant stands. The points are mean distances for each time period, calculated from relative densities (+) and relative fourth-root-transformed densities (□). The lines represent the means for the different sampling periods for relative densities (—) and relative fourth-root-transformed densities (---), respectively. All distances are scaled so that the mean distance between the youngest rehabilitating stand and the unmined forest for each time period and transformation is 1, and the mean distance between transects in the unmined forest is 0.

July 1994 are presented in Tables 5a and b, respectively. Twenty-nine species contributed 71.1%; 11 species contributed 37% of Bray-Curtis distance between the oldest rehabilitating stand and the unmined forest during October 1993 to 15 March 1994; 25 species contributed 70.4%, and 10 species 36.8%

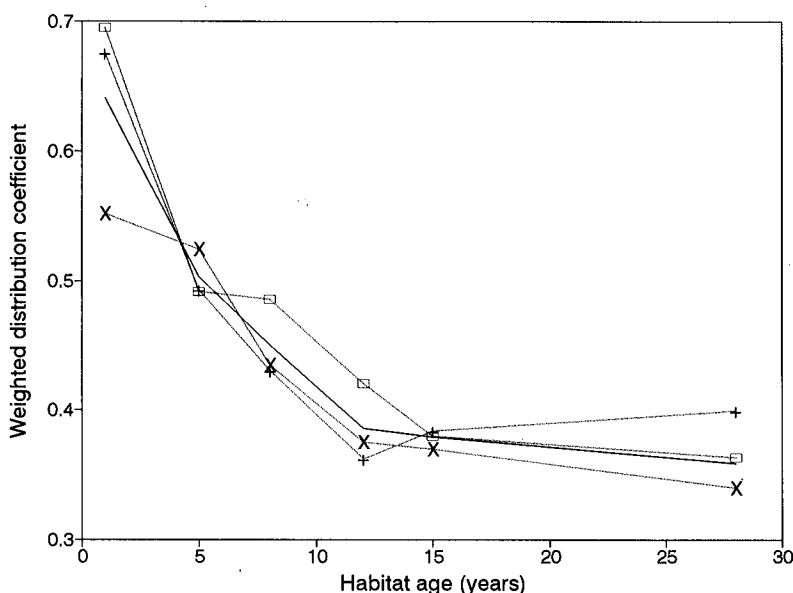


Fig. 3. The relationship between the weighted distribution coefficient and habitat regeneration age. The weighted distribution coefficient is the relative area of the southern African distribution of each species, multiplied by its density on each transect. Mean weighted distribution coefficient values in the different aged stands for the three time periods (May–September 1993, +; October 1993–15 March 1994, □; 16 March–July 1994, X) are connected by dotted lines, while the solid line is the mean for the three sampling periods.

during 16 March 1994 to July 1994. Five species were included in the top 37% during both periods, namely, Terrestrial Bulbul, Yellowbreasted Apalis, weavers (Yellow and Lesser Masked), White-eared Barbet and Bluemantled Flycatcher.

**Weighted distribution coefficient.** The weighted distribution coefficient decreased with habitat regeneration age (Fig. 3). Log-linear regression analyses revealed that the slopes of the lines describing these declines differed significantly from 0 ( $t = -2.41, -4.39$  and  $-4.41, P < 0.05, P < 0.001$  and  $P < 0.001$  for the three sampling periods, respectively).

**Discussion**

The coastal plains of KwaZulu-Natal have a long history of human disturbances. Iron Age man has been present in Moputland since at least AD 270,<sup>22</sup> and Bantu people have been practising slash-and-burn type agriculture since the 15th century. During the 19th century, the area was inhabited by the Mbonambi tribe, blacksmiths who made the ‘assegaais’ (stabbing spears) used by the Zulu king Shaka. More recently, the region has been part of the ‘homeland’ of KwaZulu, and communal ownership has been associated with subsistence agriculture and high population densities. Because some parts are inaccessible and restrictions have been imposed on habituation of the narrow coastal cordon for some 50 years, some patches of apparently mature coastal dune forests still occur. Protective measures brought about by moving people out of the area resulted in much of the vegetation of the coastal strip recovering by 1974. The wider region is known to have a very rich bird life, with 658 species recorded in the whole of KwaZulu-Natal up to 1979.<sup>23</sup>

The rehabilitating mining path where the study took place is abutted on the coastal side by a narrow (50–150-m) strip of indigenous forest with insular patches of *Casuarina equisetifolia* established some 30 years ago. Towards the interior the rehabilitating stands are bordered by a strip (100–200 m wide) of *Casuarina* plantations established over the last 10 years, which in turn lies adjacent to a relatively densely populated area dominated by subsistence farming and also fragmented through the relatively recent establishment of patches of commercial plantations.<sup>8</sup> To both the south and the north of the mining path lies a coastal strip of uninhabited forest exposed to varying levels of disturbance due to irregular grazing (mainly by cattle) and the collection of building material, firewood and medicinal plants by adjacent inhabitants. The uninhabited study area can thus be considered an island comprising different stages of coastal dune forest succession.

The development of the bird communities in the study area is taking place on its own accord and the presence of specific species reflects their ability to colonise and survive in areas representing different stages of forest development. These birds, through their feeding activities, may also aid in the dispersal

Table 5. Species discriminating between the oldest rehabilitating stand and the unmined forest based on their contribution to Bray-Curtis distances between these areas and fourth-root-transformed relative densities for each species. Species are listed in order of their mean % contribution ( $\bar{\delta}_i$ ) to the average distance between transects in the oldest rehabilitating stand and in the unmined coastal dune forest, with a cut-off point when the cumulative contribution ( $\Sigma\bar{\delta}_i$ ) reaches a value of 70%.  $\bar{\delta}_i/SD(\bar{\delta}_i)$  indicates the consistency of a species' contribution in different comparisons. Untransformed mean relative density (proportion of total density  $\times$  100) of each species is also presented.

Species	Percentage contribution towards distance				Mean relative density					
	Mean $\bar{\delta}_i$	Standard deviation $SD(\bar{\delta}_i)$	Consistency $\bar{\delta}_i/SD(\bar{\delta}_i)$	Cumulative contribution $\Sigma\bar{\delta}_i$	Stand age (years)					
					0-2	3-5	6-8	9-12	13-15	Unknown
Terrestrial Bulbul	4.2	0.61	6.8	4.2			0.12			2.60
Yellowbreasted Apalis	3.9	1.12	3.5	8.1		10.22	18.87	28.43	24.94	9.40
Bluemantled Flycatcher	3.9	0.67	5.8	12.0						1.87
Blackeyed Bulbul	3.7	0.48	7.7	15.7	1.97	0.97	0.64	6.11	7.05	1.40
Weavers (Lesser Masked & Yellow)	3.6	0.89	4.1	19.4	15.94	21.77	8.42	12.31	4.57	1.18
Southern Boubou	3.1	0.82	3.8	22.5						0.66
Squaretailed Drongo	3.1	1.82	1.7	25.5			0.07	0.09	6.14	2.08
Grey Sunbird	3.0	2.48	1.2	28.5			1.39	2.39	1.59	0.71
Pygmy Kingfisher	2.9	2.27	1.3	31.4				0.06	0.62	
Bluegrey Flycatcher	2.8	1.71	1.7	34.2			0.37	5.14	5.81	2.18
White-eared Barbet	2.7	2.08	1.3	37.0						1.82
Willow Warbler	2.6	2.08	1.3	39.6		0.25	9.88	6.98	0.75	0.14
Forktailed Drongo	2.5	2.09	1.2	42.1		0.01	0.06	1.88	0.99	0.14
Sombre Bulbul	2.5	1.95	1.3	44.6			0.27			1.12
Blackbellied Starling	2.4	1.85	1.3	47.0						0.96
Natal Robin	2.3	1.74	1.3	49.2			0.52	0.36	0.04	1.06
Garden Warbler	2.2	1.94	1.1	51.4			0.49			0.56
Rudd's Apalis	2.0	1.55	1.3	53.5			1.82			0.68
Yelloweyed Canary	2.0	2.02	1.0	55.5	0.68	0.21	0.27	0.06	0.37	0.20
Tawnyflanked Prinia	1.9	1.70	1.2	57.4	10.93	4.21	12.57	0.26	0.24	0.22
Grey Waxbill	1.9	1.94	1.0	59.3		0.15	0.54		0.26	0.21
Bleating Warbler	1.9	1.19	1.6	61.1		12.84	17.58	19.30	21.6	26.99
Brown Robin	1.8	2.74	0.7	62.9			0.17		0.65	
Puffback	1.7	0.90	1.9	64.7			0.67	2.08	4.67	4.23
Scalythroated Honeyguide	1.7	1.36	1.2	66.4						
Redeyed Dove	1.6	2.46	0.7	68.0						0.69
Tambourine Dove	1.6	1.10	1.5	69.6		0.06		0.24	0.41	0.49
Collared Sunbird	1.6	1.17	1.3	71.1			0.58	1.49	3.92	8.30
<b>b. 16 March to July 1994</b>										
Sombre Bulbul	4.4	1.41	3.1	4.4	0.36		0.21			2.29
White-eared Barbet	4.1	0.68	5.9	8.4						2.39
Redbacked Mannikin	4.0	2.55	1.6	12.4				7.49	8.79	3.19
Terrestrial Bulbul	3.7	0.68	5.5	16.1						1.20
Rudd's Apalis	3.6	1.07	3.4	19.7			0.98			1.14
Natal Robin	3.5	1.95	1.8	23.3		1.00	6.06	1.40	0.13	4.23
Weavers (Lesser Masked & Yellow)	3.5	1.32	2.6	26.7	16.92	4.63	5.58	18.16	15.97	4.25
Yellowbreasted Apalis	3.5	0.67	5.1	30.2		12.51	19.88	28.90	18.52	6.14
Longbilled Crombec	3.3	0.42	8.0	33.5			0.26		0.34	
Bluemantled Flycatcher	3.3	0.90	3.7	36.8						0.72
Bronze Mannikin	2.8	3.13	0.9	39.7			2.15	0.49	1.28	
Tawnyflanked Prinia	2.8	1.77	1.6	42.5	32.11	3.97	8.89		0.87	0.36
Blackbellied Starling	2.5	2.64	1.0	45.0				0.20	0.97	1.18
Thickbilled Weaver	2.5	1.95	1.3	47.5						1.16
Common Quail	2.5	2.75	0.9	50.0	1.52	3.32	0.82		0.89	
Wattle-eyed Flycatcher	2.5	1.97	1.2	52.4						1.51
Forktailed Drongo	2.4	0.25	9.6	54.9				3.37	1.84	0.31
Yelloweyed Canary	2.4	3.72	0.6	57.3	1.93	0.87				3.01
Olive Bush Shrike	2.3	1.83	1.3	59.6						0.79
Bluegrey Flycatcher	2.3	1.91	1.2	61.9			0.36	2.87	0.67	0.59
Redeyed Dove	2.3	2.23	1.0	64.2						0.72
Grey Waxbill	2.2	2.17	1.0	66.3			1.30	0.44	0.56	0.25
Purplebanded Sunbird	2.1	2.33	0.9	68.4				0.15	0.45	
Scalythroated Honeyguide	1.9	1.51	1.3	70.4						

of certain plants and thus influence the development of coastal dune forest vegetation.

Although species diversity has been described as a 'non-concept',<sup>24</sup> our approach of using different numerical and graphical methods to express diversity may avoid most of the pitfalls associated with the interpretation of any single method. The relevance of the different methods and indices for the present study is that temporal patterns associated with habitat regeneration in all measures of diversity were similar. The hypothesis of no increase in species diversity and species richness with habitat regeneration age was rejected; 15 years of habitat rehabilitation was associated with an increase in bird species diversity. However, diversity in the oldest rehabilitating stand was still lower than in the unmined forest. The rarefaction and rank-abundance curves for the present study support the observed pattern of increasing diversity with increasing stand age. The recorded increase in diversity is thus not an artifact of the methods of expressing it.

Many different parameters and processes can influence species diversity and several authors have attempted to explain differences in bird species diversity among areas.<sup>14,25</sup> Clear-cutting of forested or wooded areas, as in the case of the present study, inevitably leads to the destruction of vertical habitat complexity. During rehabilitation, this complexity redevelops and the increasing bird species diversity with regeneration age in forested or wooded areas can therefore be expected.

Ricklefs<sup>26</sup> showed that local diversity depends on regional diversity, and it is therefore likely that the number of species in small areas (such as those in the current study) depends on the availability of similar habitat on a regional scale,<sup>27</sup> as well as on bird diversity within that habitat. Undisturbed habitats probably dominated prior to the arrival of modern human societies and we therefore expect the bird community of the region to be dominated by species adapted to undisturbed habitats. This may explain why diversity in undisturbed areas is higher than in rehabilitating parts. With age the habitat becomes more similar to the unmined forest, resulting in colonisation by some forest species.

The null hypothesis of no increase in density with habitat regeneration age could not be rejected for any of the sampling periods. Density can be expected to increase with habitat age if the ability of rehabilitating habitat to sustain individuals rises. This expectation does not apply consistently, however, as some pioneer taxa may respond positively to disturbance (for instance, by small mammals<sup>28</sup>). Furthermore, along a temporal habitat gradient densities of individual species will not show simply monotonic changes, so that it is unlikely that total density will follow a distinct trend, unless very few species are numerically dominant throughout the area or all species are restricted by a few limiting resources.

As in the present study, several authors found a non-uniform increase in density with habitat age, that is, an increase followed by a decrease and sometimes a further rise to the highest densities in mature forest.<sup>28,29</sup> The density of a species could be determined by resource levels but this only holds when resources are limiting. Although this has often been assumed, density can be maintained below the levels at which resources become limiting through predation,<sup>30,31</sup> disturbance and environmental variation.<sup>32</sup> Recently, the influence of adjacent communities, or even those further afield, has been noted.<sup>33</sup> Shugart and James<sup>1</sup> ascribed the low densities in middle-late stages of succession to uniform habitats, but this is unlikely to be the case in the present study, as areas with high densities (6–8 years old) also appear very uniform.

The decreasing turnover rate with increasing regeneration age recorded during the present study is expected to occur in keeping with succession theory.<sup>34</sup> This decreased turnover rate is responsible for the concept of a 'climax', where a climax is the state reached when the rate of succession (turnover rate) has decreased to an imperceptible level.<sup>1</sup> The development of the avian community of these coastal dune forests is well described by identifying species typical of each stand. Multidimensional scaling showed that older rehabilitating stands become increasingly similar to the unmined stand, and gave an overall impression of the developing avifauna.

The analysis of discriminant species reflects on variations in species composition between different stands, and thus shows which species are responsible for community changes. The analysis centred on species discriminating between the oldest rehabilitating stand and the unmined forest. Here we consider only the 10 species that contributed most to the Bray-Curtis distance during the sampling periods October 1993 to 15 March 1994 and 16 March 1994 to July 1994. Of the 16 species included (four were included in both time periods), nine peaked in relative abundance in the older rehabilitating stands (9 years and older) and may therefore be considered mid-successional species. Two species (Rudd's Apalis and Natal Robin) peaked in the rehabilitating stands at around 8 years of age, after which they declined, but showed a second peak in the unmined forest. The remaining five species occurred mainly in the unmined forest. Four of the five (as well as Rudd's Apalis and Natal Robin) were associated with a dense shrub and sapling (undergrowth) layer. The thickets of the 8-year-old rehabilitating stand seem to be similar to the undergrowth layer of the unmined forest, as they consist of a high density of vegetation in the lower 2–4 m, which was absent in the older rehabilitating stands.<sup>11</sup>

The last discriminant species of the 16 is the White-eared Barbet, which is a self-excavating hole nester. Densities for all hole nesters (woodpeckers, barbets and hornbills) followed a similar trend, with the smallest species (Goldenrumped Tinker Barbet) occurring in the older rehabilitating stands. The others, of which the White-eared Barbet was the most common, were absent from all rehabilitating areas. This can be explained by the absence of suitable branches for nesting. It therefore seems that differences in the avifauna between the oldest rehabilitating stands and the unmined forest are related to environmental factors. Two of those that seem to be important are the presence of undergrowth and of large, old trees.

It is generally accepted that widespread species are ecologically generalised.<sup>35</sup> The weighted distribution coefficient is therefore considered a useful 'index of generalisation', as opposed to specialisation. This is based on the assumption that birds with a wider distribution will inhabit a wider range of habitats, but in the case of this study is somewhat confounded by the fact that forests cover a very small part of southern Africa (0.2% or less than 3000 km<sup>2</sup>, ref. 36) when compared to woodland, savanna or grassland. A grassland specialist will therefore have a wider distribution than a forest specialist, but still narrower than a habitat generalist. The youngest stand can be considered to be representative of the grassland biome, and high WDC values in this stand should be expected. The decreasing WDC with stand age (even excluding the youngest stand) therefore indicates an increase in forest specialists. The data used were also obtained from general-purpose distribution maps; errors due to cartographic inaccuracies are not likely to be of importance. The clear decrease in WDC with increase in habitat age rejects the null hypothesis that generalists will not be replaced by specialists (in

this case habitat specialists), or species with a narrower niche,<sup>4</sup> during habitat development.

## Conclusion

The changes in bird community composition of rehabilitating coastal dune forests at Richards Bay support theoretical models of succession, and are remarkably similar to other studies on forest succession. Well-documented relationships exist between habitat structure and bird species diversity as well as between species richness or diversity and area of a specific habitat in a region. On the other hand, total (community) density is a result of many different factors selectively influencing the populations of many different species. The increasing importance of species with a restricted distribution suggests that we can predict some of the changes in species composition that take place during succession, even without knowledge of the particular species involved.

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1. Shugart H.H. Jr. and James D. (1973). Ecological succession of breeding bird populations in northwestern Arkansas. *Auk* **90**, 62–77.
2. May P.G. (1982). Secondary succession and breeding bird community structure: patterns of resource utilization. *Oecologia* **55**, 208–216.
3. Blondel J. (1983). The dynamics of bird communities along mainland and island Mediterranean successions. *Ibis* **125**, 588–589.
4. Odum E.P. (1969). The strategy of ecosystem development. *Science* **164**, 262–270.
5. Karr J.R. (1968). Habitat and avian diversity on strip-mined land in east-central Illinois. *Condor* **70**, 348–357.
6. Mönkkönen M. and Helle P. (1987). Avian reproductive output in European forest successions. *Oikos* **50**, 239–246.
7. Pickett S.T.A. (1976). Succession: an evolutionary interpretation. *Am. Nat.* **110**, 107–119.
8. Van Aarde R.J., Ferreira S.M., Kritzing J.J., van Dyk P.J., Vogt M. and Wassenaar T.D. (1996). An evaluation of habitat rehabilitation on coastal dune forests in northern KwaZulu-Natal, South Africa. *J. Restoration Ecol.* **4**, 334–345.
9. Mentis M.T. and Ellery W.N. (1994). Post-mining rehabilitation of dunes on the north-east coast of South Africa. *S. Afr. J. Sci.* **90**, 69–74.
10. Wiens J.A. (1989). *The Ecology of Bird Communities*, vol. i. *Foundations and Patterns*. Cambridge University Press, Cambridge.
11. Kritzing J.J. (1996). *Avian community structure on rehabilitating coastal dune forests in northern KwaZulu-Natal, South Africa*. MSc thesis, University of Pretoria.
12. Buckland S.T., Anderson D.R., Burnham K.P. and Laake J.L. (1992). *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London.
13. Laake J.L., Buckland S.T., Anderson D.R. and Burnham K.P. (1993). *DISTANCE User's Guide V 2.0*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins.
14. James F.C. and Wamer N.O. (1982). Relationship between temperate forest bird communities and vegetation structure. *Ecology* **63**, 159–171.
15. James F.C. and Rathbun S. (1981). Rarefaction, relative abundance, and diversity of avian communities. *Auk* **98**, 785–800.
16. Ludwig J.A. and Reynolds J.F. (1988). *Statistical Ecology: a Primer on Methods and Computing*. Wiley-Interscience, New York.
17. Tokeshi M. (1993). Species abundance patterns and community structure. *Adv. Ecol. Res.* **24**, 111–186.
18. Kruskal J.B. and Wish M. (1978). *Multidimensional Scaling*. Sage, Beverley Hills, California.
19. Bray R.J. and Curtis J.T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecol. Mono.* **27**, 325–349.
20. Clarke K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **18**, 117–143.
21. Maclean G.L. (1993). *Roberts' Birds of Southern Africa*, 6th edn. John Voelcker Bird Book Fund, Cape Town.
22. Bruton M.N., Smith M and Taylor R.H. (1980). A brief history of human involvement in Maputaland. In *Studies on the Ecology of Maputaland*, eds. M.N. Bruton and K.H. Cooper, pp. 432–459. Rhodes University, Grahamstown and the Natal Branch of the Wildlife Society of Southern Africa, Durban.
23. Cyrus D. and Robson N. (1980). *Bird Atlas of Natal*. University of Natal Press, Pietermaritzburg.
24. Hurlbert S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**, 577–586.
25. Willson M.F. (1974). Avian community organization and habitat structure. *Ecology* **55**, 1017–1029.
26. Ricklefs R.E. (1987). Community diversity, relative roles of local and regional processes. *Science* **235**, 167–171.
27. Karr J.R. (1976). Within- and between-habitat avian diversity in African and neotropical lowland habitats. *Ecol. Mono.* **41**, 207–233.
28. Ferreira S.M. and van Aarde R.J. (1996). Changes in community characteristics of small mammals in rehabilitating coastal dune forests in northern KwaZulu-Natal. *Afr. J. Ecol.* **34**, 113–130.
29. Westworth D.A. and Telfer E.S. (1993). Summer and winter bird populations associated with 5 age-classes of Aspen forest in Alberta. *Can. J. for. Res.* **23**, 1830–1836.
30. Martin T. (1988). Habitat and area effects on forest bird assemblages — is nest predation an influence? *Ecology* **69**, 74–84.
31. Møller A.P. (1991). Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. *Ecology* **72**, 1336–1349.
32. Wiens J.A. (1977). On competition and variable environments. *Am. Scientist.* **65**, 590–597.
33. Furness R.W., Greenwood J.J.D. and Jarvis P.J. (1993). Can birds be used to monitor the environment? In *Birds as Monitors of Environmental Change*, eds R.W. Furness and J.J.D. Greenwood. Chapman and Hall, London.
34. Myster R.W. and Pickett S.T.A. (1994). A comparison of rate of succession over 18 years in 10 contrasting old fields. *Ecology* **75**, 387–392.
35. Bowers M.A. (1988). Relationship between local distribution and geographic range of desert heteromyid rodents. *Oikos* **53**, 303–308.
36. Siegfried W.R. (1984). Preservation of species in southern African nature reserves. In *Biotic Diversity in Southern Africa: Concepts and Conservation*, ed. B.J. Huntley, pp. 186–201. Oxford University Press, Cape Town.