



The contribution of the bird community of the regenerating coastal dunes at Richards Bay to regional diversity

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Dedicated to my parents

**The contribution of the bird community of the regenerating
coastal dunes at Richards Bay to regional diversity**

by

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Abstract

Habitat modification in response to disturbances such as slash-and-burn agriculture, afforestation, deforestation and mining affects local communities. Such effects depend on the scale of the disturbances. The present study shows that deforestation, afforestation, the neglect of afforested areas, and dune rehabilitation reduce the total density, richness and diversity of bird communities. Vegetation regeneration in response to a 23 year long rehabilitation programme gave rise to habitats that supported birds assemblages that with age increased in similarity to those typical of undisturbed dune forests. Habitat rehabilitation facilitated local colonisation and local extinction patterns typical of ecological succession, with generalists (small-bodied, seed-eaters) being the first to colonise new habitats (grasslands and scrublands). Habitat specialists such as fruit-eating, hole-nesters were the last to colonise regenerating habitats. Patterns in local and in regional diversity could not be explained through the Intermediate Disturbance Hypothesis. Increased richness, diversity and total density with decreased levels of habitat disturbances appears to be driven by habitat heterogeneity. Assemblages of rehabilitating areas did not differ from those of disturbed landscapes in the region. Habitat rehabilitation thus does not impair the characteristics of bird communities of the northeast coastal region of KwaZulu-Natal, South Africa.

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Chapter 1

General introduction

Rationale for present study

Human induced environmental disturbances are often followed by a restoration or rehabilitation orientated program aimed at establishing a defined “indigenous ecosystem”. As such, the purpose of such programs is to improve ecosystem structure and function. In theory programs strive to restore a disturbed system to its pre-disturbance, though in reality only partial success can be achieved (Bradshaw 1990). Therefore, any resemblance of the post-rehabilitation community structure to that of the pre-disturbance state indicates some success in the rehabilitating program. Such success can be regarded as the development of communities from simpler to a more complex state (Van Aarde *et al.* 1996a, 1996b).

The post-mining rehabilitation of coastal dune vegetation north of Richards Bay on the north coast of KwaZulu-Natal, South Africa has given rise to the development of a series of spatially separated patches of indigenous vegetation of known age. Previous studies have shown that several taxa on these sites have developed along similar pathways through time (Van Aarde *et al.* 1996a, 1996b, Ferreira & van Aarde 1997, Kritzing & van Aarde 1998). For example, Kritzing and van Aarde (1998) suggested that bird community structure on the regenerating coastal dunes develop towards those recorded for bird communities on nearby “bench-mark” sites. They also suggested that different disturbance events (such as clearcutting, grazing, afforestation of exotic timber plantations and burning) may have different consequences for the development of bird assemblages within the region. Some of these disturbed patches of regenerating vegetation or afforested plantations mimic successional patterns that occur on the post-mining regenerating areas (Mentis & Ellery 1994). The disturbance gradient in the region also may have consequences for bird assemblages, either by enhancing species richness, or by lowering species richness through negatively affecting rare species typically occurring at low densities in relatively undisturbed areas. The bird assemblages on the regenerating coastal dune vegetation may also further augment diversity

towards the region or be totally atypical with the ideals set for the maintenance of biodiversity in the region.

The present study, which considers the avifauna specifically, has several key aims. These include (a) a comparison of the present bird community structure on the regenerating sites of coastal dune forest with those sampled five years ago (Chapter 3), (b) an examination of the effect of habitat disturbance on patterns of species diversity (Chapter 4), and (c) an evaluation of the contribution of the bird community of the regenerating coastal dune forest to regional diversity (Chapter 5). As such the study relies on a series of ecological principles and variables, which are discussed below.

Ecological succession

Succession determines the development of most community patterns and may be regarded as a non-seasonal, directional and continuous pattern of colonisation and extinction of a local area by species populations. Succession usually occurs after some environmental disturbance event. A range of alternative types of serial replacements has given rise to different patterns of ecological succession (Begon *et al.* 1986). Degradative succession occurs when a degradable resource is utilised successively by a number of species. One species would invade the system, remove the available resources, and generate other resources which are then available to other species. As such, degradative succession relies on a species modifying the physical condition of the resource to favour the next species. Since heterotrophic organisms are involved in such sequences of succession it is often referred to as heterotrophic succession.

Alternatively, allogenic succession may occur when a new habitat is created, not degraded, but simply occupied by a species. The new habitat would be modified and consequently made accessible to a new species for colonisation. The serial replacement of a species in allogenic pathway would be governed by external geophysical-chemical forces. A third successional pathway, autogenic succession, usually occurs when both the environment and the community change through biotic processes. During early succession, a colonist species may alter the conditions of the environment, for instance by making resources available for another species to colonise. This alternation of conditions, which favours the colonisation by another species, is known as facilitation and the inverse as inhibition.

Several models have been proposed to clarify the mechanism of autogenic succession. Horn (1981) developed a tree-by-tree replacement process, by establishing the probability of a certain tree species being able to colonise a specific area at a specific time interval. Connell & Slatyer (1977) produced the facilitation, tolerance and inhibition models, of which the first two models have been described above. According to the tolerance model, a modification of the habitat by early colonists will have little effect on recruitment of later successional species. On the other hand, Tilman (1988) placed emphasis on the continual changing of competitive abilities of species as the underlying mechanism of succession.

Studies evaluating the regeneration of coastal dune forests in my study area in KwaZulu-Natal, South Africa, have confirmed that a broad spectrum of communities, including birds, converge in similarity towards those typical of an undisturbed forest in the region (Kritzinger & van Aarde 1998, Van Aarde *et al.* 1996a, Van Aarde *et al.* 1996b). The pattern of the recorded convergence in this system implied that development is dictated by ecological succession. As part of a study on birds in developing forest in North America, May (1982) concluded that the number of feeding guilds, species density, and species richness increase as vegetation structure became more complex through time. Similar patterns have been noted by Kritzinger & van Aarde (1998) for bird communities on the rehabilitating coastal dune forests at Richards Bay.

Community energetics, such as the ratio between production:community respiration, production:biomass and production:consumption decreases with an increase in successional state (Smith & MacMahon 1981, Wilson & Keddy 1988, Tilman *et al.* 1996). In addition, life history traits such as the size of an organism are expected to increase, and selection pressures should revert from *r*- to *K*-selection (Odum 1969, Smith & MacMahon 1981). Furthermore, in birds specifically, reproductive output should decrease with successional progress due to the greater incidence of multiple-brooding and increasing stability (May 1984, Mönkkönen & Helle 1987).

Species diversity

The number of species in ecological communities varies in time and space (Begon *et al.* 1986). The concept species diversity is a function of two integrating concepts; first the number of species contained within a specified community (species richness), and second the distribution of individuals among these species (evenness) (James & Rathbun 1981). However, as species

density measured across space increases, species richness also tends to increase due to the increased number of field observations. For this reason Hurlbert (1971) has criticised diversity measures (e.g. Shannon-Wiener diversity index and Simpson's measure of concentration), for their insensitivity towards rare species within community assemblies, describing species diversity as a "non-concept". Besides this conceptual problem, a range of alternative parameters (e.g. rarefaction) has been developed to disconnect information theory and the meaningless descriptors of biological properties (Heck *et al.* 1975, James & Wamer 1982). Species diversity is essentially a structural concept and cannot be separated from the theories of community organisation (Hill 1973). Diversity is a measurable parameter and the observed values may be explained by a variety of theories.

Most studies have been described at the within-community scale and regarded as communities existing at a particular locality of homogenous nature. Such a community is a true reflection of the vegetation structure of a particular habitat (Cody 1981). Nevertheless, this observed α -diversity is not the only important component of species diversity. Communities are dynamic when viewed across a range of spatial scales and the patterns of species assembly change continuously across environmental gradients (Drake 1990a, Drake 1990b). The rate of species turnover between habitat types constitutes the β -diversity, a function that may explain the difference between habitat types, their size and contiguity. At a larger scale, γ -diversity describes the rate of species turnover within a habitat type between different communities. γ -diversity is therefore a function of locality segregation and of intervening barriers to species dispersal (Cody 1994).

Factors that have been attributed to shape diversity patterns include environmental stability and predictability (McArthur 1965, Begon *et al.* 1986), productivity (Pianka 1966, Currie 1991), non-equilibrium interactions of competing species populations (Huston 1979), latitudinal gradients (Rosenzweig 1992), and species-area curves (Wiens 1989). Unfortunately, most of these explanations lack supporting evidence and include a degree of circular reasoning (Rohde 1992). However, Currie (1991) showed that environmentally available energy (such as high potential evapotranspiration) correlates with species richness. Schluter & Ricklefs (1993) summarise six possible types of processes that may explain patterns in diversity:

1. Local interactions within a uniform habitat may contribute to diversity theory. Both competitors and predators reduce the apparent diversity of taxa through elimination, and act to constrain local diversity, without providing any explanation for the regional production of species. On the other hand, α -diversity or local diversity has been explained as being linear to regional diversity (γ -diversity). Therefore, as long as local communities remain unsaturated (non-interactive), regional processes will determine the richness of local communities (Caley & Schluter 1997). Ricklefs (1987) concludes that the linear addition of species from a regional pool to enhance the local species richness of communities depends on local processes such as competitive exclusion, predation, adaptation, and chance effects. Cornell (1985a,b) studied cynipine gall wasps on oaks (*Quercus* spp.) and concluded that the strength of local interactions could be used to predict linearity between local and regional diversity, e.g. strong local interactions will promote species specialisation and niche heterogeneity, with the result that all available niche space is occupied, and the community reaches saturation. Shorrocks & Sevenster (1995) and Cornell & Lawton (1992) inferred that local unsaturated (non-interactive) communities are ubiquitous and saturation may not persist through the spatio-temporal heterogeneity observed in most natural communities.
2. Diversity is influenced by movement of individuals between patches of the same type of habitat, but underscores the dynamic nature of a local community and external processes of local populations.
3. Dispersal between habitats such as mass effects, rescue effects and source-sink dynamics reflect the interdependence of local and regional diversity. Here species are not self-maintaining but only co-exist through contact transitions between different habitats (Shmida & Wilson 1985). In addition, ecological equivalence also demonstrates the co-existence of species with similar niche and habitat requirements when their habitats overlap, effectively promoting diversity (Shmida & Wilson 1985). These processes are most important at the regional and landscape scale.
4. Diversity also gains subsistence through the spread of taxa within regions of their habitat of origin. Taxa originate and diversify within a certain type of habitat and require evolutionary change to expand into other habitat types. There exists a

- relationship between habitat and diversity that is dependent on both the size and history of the habitat. These considerations recognise community development.
5. Particular geographic configurations of habitats, such as climate and vegetation structure, differ in their influence on species dispersal. This has a marked influence on species evolution. This type of speciation is known as allopatric production of species (Rosenzweig 1992).
 6. Unique events such as episodes of catastrophic extinction (e.g. Pleistocene glaciation) reduce diversity and constrain cladogenesis.

The contribution of species diversity towards community function and composition

Theoretically species diversity has always been regarded as the number of species within a community and the equitability of the number of individuals of each species (Hurlbert 1971, Tramer 1969). In addition to species richness, the composition of a community contributes to the functioning of the community as a whole (Symstad *et al.* 1998). Some species are more productive and therefore more efficient than others in the community and contribute as “core species”. Most communities consist of a hierarchy of species with a functional identity, and the species with the highest ranking in the assembly will be responsible for most of the community function. If species richness is lowered, for example through an environmental factor leading to extinction (habitat fragmentation), productivity will decrease (Aarson 1997, Tilman 1997). Several studies have revealed this correlation with plant species richness and ecosystem productivity, stability and sustainability (Naeem *et al.* 1994, Tilman *et al.* 1996, Tilman & Downing 1994).

Biomass is an effective predictor of community productivity. Expressing communities in terms of species-specific biomass can help identify the keystone species responsible for the most productive contribution towards community function (Brewer *et al.* 1997). Biomass should change as succession proceeds, because the different species that invade the system have different abundances and body masses (Wilson & Keddy 1988). Wiens (1986) stated that larger species have a greater effect on, for instance, resource consumption than smaller-sized species. In terms of bird communities, the non-passerine species populations (with greater body mass) tend to be more stable and efficient at exploiting larger resources than the smaller resources exploited by smaller passerines with high mass-specific metabolisms (May 1982).

Species may distribute themselves along niche dimensions in a non-random manner and these groups of species cluster together to form ecological guilds. These guilds consist of syntopic species with comparable niche requirements (rather than similar taxonomy) that exploit similar resources in a similar manner (Wiens 1986). The identification of guilds would contribute to a better understanding of the relevant importance of species richness within the target community. Therefore, a more diverse (in term of species richness) community will consist of more ecological guilds through the process of finer resource exploitation. Guild structure should therefore provide a mechanism in maintaining community structure in term of species-specific contribution towards community productivity (Holmes *et al.* 1979).

Correlates of species diversity in bird communities

The floristic properties of plants and the their additive contribution towards habitat diversity has been one of the best predictors of bird species richness (Erdelen 1984, Willson 1974). Therefore bird species richness correlates with plant species richness (Cody 1981), although several other vegetation characteristics are better predictors of bird species richness (Erdelen 1984). Thus, foliage height diversity may be a better predictor of species numbers (Willson 1974, MacArthur & MacArthur 1961, Wiens 1989, MacArthur 1964). Foliage height diversity increases the vertical layering (vertical stratification), thereby creating a niche dimension in a vertical plane. This would enable more species, including potential competitors, to co-exist. (MacArthur *et al.* 1966). Erdelen (1984) and Roth (1976) investigated horizontal variability in habitat profiles (patchiness) as an important factor influencing bird species diversity. They introduced the concept of structural diversity through addition of vertical diversity and horizontal diversity. The above indices provide information about the spatial distributions of bird species in vegetation.

Chapter 2

Materials and Methods

Study area

The study area is located within the eastern coastal plain of KwaZulu-Natal, South Africa. It forms part of the Tongaland-Pondoland regional mosaic that extends from the Limpopo River in the north (25°S) to Port Elizabeth (34°S) in the south. The area consists of Cretaceous and Tertiary marine sediments that comprise mostly of unconsolidated brown sandy soils (White 1983). The climate is subtropical, hot and humid, with high summer temperatures when mean values exceed 30°C for about 26 days per annum. The winters are moderate with the lowest mean monthly temperature being 13.4°C. The rainfall is evenly distributed throughout the year, with 60% of the total precipitation recorded between October and March. Relative humidity is high in summer, with a monthly mean of 79-88% at 08h00 and 61-74% at 14h00. Humidity drops to below 70% in winter (Venter 1976, Kritzing 1996).

The area consists of vegetated sand dunes that run parallel to the coastline and are commonly referred to as coastal dune forests. At the time of the study the area between Richards Bay (28°30'S 32°25'E) and Cape Vidal (28°11'S 32°33'E) consisted of patches of relatively mature forest, patches of unmined and post-mined regenerating dune vegetation and patches maintained by fire as grasslands. Some of the areas between these patches of indigenous vegetation comprise exotic plantations, while others have been invaded by alien vegetation. Common species on these exotic plantations include pine (*Pinus elliotii* (L.)) and gum (*Eucalyptus grandis* (L'Her)) trees. Some other areas in the region have been disturbed either through clearance (pre-mining activities, felling) or the establishment of beefwood (*Casuarina equisetifolia* (J.R. & G.Forster)) plantations. The study area can thus be seen as a mosaic of patches of indigenous and exotic vegetation of which most of the indigenous patches are in a transitional stage of successional development. Kritzing (1996), Kritzing & van Aarde (1998) and van Aarde *et al.* (1996a, 1996b) give full descriptions of the mining operation

and dune rehabilitation programme that have given rise to the development of the coastal dune vegetation sere that developed in response to post-mining dune rehabilitation.

Study sites

A series of study sites were established as in the following areas:

1. Six sites in known-aged, post-mining regeneration areas (1-4, 5-8, 9-11, 12-14, 15-18 and 19-21 years old)
2. Two unmined sites representing “bench-mark” communities (mature dune forest vegetation at Zulti/Sokhulu and Mapelane) and one site representing a 32-37 years old coastal foredune community.
3. Four unmined, developing indigenous plant communities.
4. An area maintained as an indigenous grassland (Cape Vidal/St. Lucia).
5. Three different exotic plantations (pine, gum and neglected beefwood plantations).

The location of each of these sites is presented in Figure 1 and descriptions of their floristic compositions are provided in Table 1 and 2.

Data collection

Data were collected during two study periods, separated by five years (1993/94 and 1998/99). The 1993/94 databases were obtained from the data files of the Conservation Ecology Research Unit (CERU, University of Pretoria). These data were collected using the methods described by Kritzing (1996) and Kritzing & van Aarde (1998). Data were collected along fixed line transects with a minimum length of 250 m in order to ensure sufficient observations ($n \geq 30$) could be obtained for correct and unbiased density estimates (Buckland *et al.* 1992). During 1998/99 the number of transect lines surveyed in a given study site varied from 3 to 8 depending on the area of the sites being sampled (see Table 3). During the 1993/94 study period five rehabilitating sites were sampled (3 transect lines per site, except for the youngest site and the 32-37 year old site, where only one transect line was sampled) (see Table 3).

Transects were located at least 200 m apart to improve the independence of observations. Within each site starting points were randomised to facilitate the independence of sampling. Transect lines were surveyed for a period of four hours, beginning 30 – 60 minutes after sunrise, when the birds were most active and conspicuous. When surveying a transect line data collected include the identification of each bird seen on the line (considered a single

observation point), the number of individuals of each species seen during each observation (group size), the distance between the observer and the bird/group, and the compass bearing between the bird/group and the transect line for each observation. All distances from the observer to the bird were measured using a “Telinject Ranging TLR 75” rangefinder (Telinject, USA, 9316 Soledad Canyon Road, Sougus, California 91350) and all bearings were measured with a “Suunto” compass (Suunto Oy, Valimotie, FIN-01510, Vaanta, Finland). All observations further than 60 m perpendicular to the transect line were truncated due to the expected monotonic decrease in detectability. In order to standardise data collection, all birds were recorded where they were first seen perching or sitting and all transects were traversed within a one hour period.

The probability of seeing a bird at a specified distance from the line is a function of the distance from the transect line. The software package DISTANCE (Laacke *et al.* 1993) was used to convert observations to total density of birds (density/ha) for each sampled site. The package fits different detection functions of different distributions, making the model very robust. The program obtain density estimates for each transect by selecting for the most appropriate model to fit the observed detection probability function by utilising Akaike’s information criterion (Akaike 1973, Buckland *et al.* 1992). Other benefits of the package include its pooling robustness (data affecting detection probabilities can be pooled), shape criteria (used to fit different detection functions) and high estimator efficiency with model selection. In order to calculate reliable estimates of density, the following assumptions must be met with regard to data collection (Buckland *et al.* 1994):

1. All birds on the transect must be seen and correctly identified. This assumption is almost impossible to meet in the field as some birds in the nearby vicinity may be overlooked due to the high canopy and low visibility at some places. Therefore, I can only assume that the portion of birds seen on the transect line represent the total community on the transect line.
2. All birds must be recorded at the initial location on the line. All movements of the birds were random and therefore natural in relation to the movements of the observer. None of the birds moved in response to the observer presence and birds flying past without landing were omitted from the analysis. Therefore, no bird was recorded more than once.

Table 1: The vegetation characteristics of the post-mined regenerating sites included in the present study.

Years when regeneration commenced	Age of site (years)	Vegetation description
1993-1996	1-4	Secondary grassland with <i>Acacia karroo</i> Hayne shrubs scattered throughout the site. The vegetation is composed of the grass <i>Panicum maximum</i> Jacq. and important herbs such as <i>Neonotonia wightii</i> Lackey, <i>Gloriosa superba</i> L. and <i>Canavalia roseae</i> D.C.
1990-1992	5-8	<i>Acacia karroo</i> shrubland of approximately 4 meters high with various grass species as undergrowth. Woody species include <i>Dodonea unguistifolia</i> Benth. and <i>Chrysanthemoides monolifera</i> Norl. The undergrowth consists of grass species <i>Digitaria diversinervis</i> Stapf. and <i>Dactyloctenium australe</i> Steud.
1988-1990	9-11	<i>Acacia karroo</i> thicket of approximately 9 meters with sparse undergrowth. Other woody species include <i>Dodonea unguistifolia</i> , <i>Vepris lanceolata</i> G.Don and <i>Brachyleana discolor</i> DC., all characteristic of coastal dune shrub. The undergrowth (if occurring) consists primarily of and herbs such as <i>Drimiopsis maculata</i> Lindl., <i>Zehneria scabra</i> Sond. and <i>Commelina</i> spp. L.
1985-1987	12-14	Secondary dune forest with some woody species. <i>Acacia karroo</i> dominated canopy of approximately 12-13 meters in height. <i>Brachyleana discolor</i> , <i>Kraussia floribunda</i> Harvey, <i>Canthium inerme</i> Kuntze, <i>Vepris lanceolata</i> , <i>Scutia myrtina</i> Kurz. And <i>Rhus nebulosa</i> Schönl. form the major woody species of this sere. The undergrowth consists of <i>Dactyloctenium australe</i> , <i>Laportea pendularis</i> Chew. and <i>Asystasia gangetica</i> T.Anders.
1981-1984	15-18	Secondary dune forest dominated by <i>Acacia karroo</i> with a canopy 17-18 meters high. Other woody species include, <i>Mimosops caffra</i> E.Mey., <i>Celtis africana</i> Burm.f., <i>Trema orientalis</i> Blume, <i>Brachyleana discolor</i> , <i>Apodytes dimidiata</i> E.Mey., <i>Vepris lanceolata</i> and <i>Trichelia emetica</i> Vahl. The groundcover consists mostly of <i>Digitaria diversinervis</i> , <i>Laportea pendularis</i> and <i>Achyranthes aspera</i> L.
1978-1980	19-21	Forest dominated by <i>Acacia karroo</i> of 19-20 meters tall. Some of them start to fall over. The woody species are much the same than those for the 15-18 year old site. Other woody species include <i>Carissa macrocarpa</i> A.DC., <i>Draceana aletriformis</i> C.Koch, <i>Zanthoxylum capensis</i> Harv., <i>Allophylus natalensis</i> , <i>Deinbollia oblongifolia</i> Radlk., <i>Sideroxylon inerme</i> L. and <i>Psychotria capensis</i> Vatke. The groundcover consists of <i>Laportea pendularis</i> , <i>Asystasia gangetica</i> , <i>Digitaria diversinervis</i> , <i>Pupalia lappacea</i> A.Juss., <i>Senecio deltoideus</i> Less. and <i>Secamone filiformis</i> R.Br.

Table 2: The vegetation characteristics of the unmined study sites.

Name of locality	Vegetation description
Zulti/Sokhulu	An unmined forest (benchmark site) with woody species such as <i>Mimosops caffra</i> E.Mey, <i>Celtis africana</i> Burm.f. and <i>Ziziphus mucronata</i> Willd. of over 30 meters forming the canopy. Other woody species include <i>Croton sylvaticus</i> Hochst., <i>Gymnosporia mossambicensis</i> Blakelock, <i>Chaetacme aristata</i> Planch., <i>Englerophytum natalense</i> Heine & Hemsl., <i>Cordia caffra</i> Sond., <i>Drypetes natalensis</i> Hutch., <i>Ochna arborea</i> Burch., <i>Diospyros natalensis</i> Brenan., <i>Erythroxyllum emarginatum</i> Thonn., <i>Strychnos gerrardii</i> Verdoorn, <i>Teclea gerrardii</i> Verdoorn, <i>Vangueria randii</i> S.Moore, <i>Clausena anisata</i> Hook.f., <i>Chionanthus peglerae</i> Stearn and <i>Trichilia dregeana</i> Sond. The understory consists mostly of <i>Asparagus falcatus</i> L., <i>Isoglossa woodii</i> C.B. Cl., <i>Scadoxus puniceus</i> Friis & Nordal, <i>Tragia glabrata</i> Kuntze, <i>Pyrenacantha grandiflora</i> Baill. and <i>Cynanchum ellipticum</i> R.A.Dyer.
Mapelane	A natural reserve ("benchmark" site) with much the same plant species composition as Zulti/Sokhulu. Exceptions include canopy species such as <i>Albizia adianthifolia</i> Wight and uncommon species such as <i>Cussonia spaeerocephala</i> Strey and <i>Ficus natalensis</i> Hochst. The grass <i>Setaria megaphylla</i> Dur. & Schinz and the herb <i>Isoglossa woodii</i> predominate the forest floor (for a full floristic description of Mapelane see Venter 1976).
Neglected plantations	The area consists of the remnant exotic <i>Casuarina equisetifolia</i> , while alien weeds such as <i>Lantana camara</i> L. invades much of the area. Indigenous woody species include <i>Passerina filiformis</i> L., <i>Euclea natalensis</i> A.DC., <i>Clerodendrum glabrum</i> E.Meyer, <i>Bersama lucens</i> Szyszyl. and <i>Polygala myrtifolia</i> L. Much of the area is covered with the fabid creeper <i>Canavalia rosea</i> D.C.
Pine plantations	Timber species <i>Pinus elliotii</i> L. dominate the canopy, while the exotic weeds <i>Lantana camara</i> and <i>Psidium guajava</i> L. predominate in the understory. Indigenous tree species that manage to survive in this locality are <i>Peddiea africana</i> Harv., <i>Annona senegalensis</i> Pers. and a few <i>Macaranga capensis</i> Benth.
Gum plantations	Timber species <i>Eucalyptus grandis</i> L'Her. and the exotic weeds <i>Lantana camara</i> and <i>Psidium guajava</i> dominate. Indigenous tree species that manage to survive in this locality are <i>Annona senegalensis</i> , <i>Tricalysia sonderiana</i> Hiern. and <i>Kraussia floribunda</i> Harvey.
Eastern Shores (includes Cape Vidal/St. Lucia)	Typical grasslands on sand dunes with few shrubs scattered throughout the area. See Weisser (1980) for a more detailed description of the vegetation Cape Vidal and St. Lucia.
32-37 years old site	Plant species consist mostly of saltspray tolerant species. These include tree species such as <i>Strelizia nicolai</i> Regel & Koern, <i>Mimosops caffra</i> , <i>Brachyleana discolor</i> DC., and <i>Allophylus natalensis</i> De Wint.

Table 3: The number of transect lines surveyed, their lengths and the area of the sampling sites.

Study sites (age in years)	Area of sampling site (ha)	Total length of transect lines (m)	Number of transect lines	
			1993/94	1998/99
Post-mined regenerating sites				
1-4	61	1500	1	3
5-8	70	1000	3	4
9-11	86	1000	3	4
12-14	74	1000	3	4
15-18	82	1000	3	4
19-21	62	1000	-	4
Unmined sites				
32-37 years	63	1000	1	4
Zulti/Sokhulu ("bench-mark")	320	2000	-	8
Mapelane ("bench-mark")	250	1250	-	5
Neglected plantations	86	2500	-	5
Pine plantations	94	2500	-	5
Gum plantations	77	2500	-	5
Cape Vidal/St. Lucia	66	2500	-	5
5-8*	50	500	-	2
9-11*	39	500	-	2
19-21*	44	250	-	1

* Estimate of age based on information from regenerating sites of known age and physiognomic characteristics of the site, such as diameter of stem at breast height of dominant tree species.

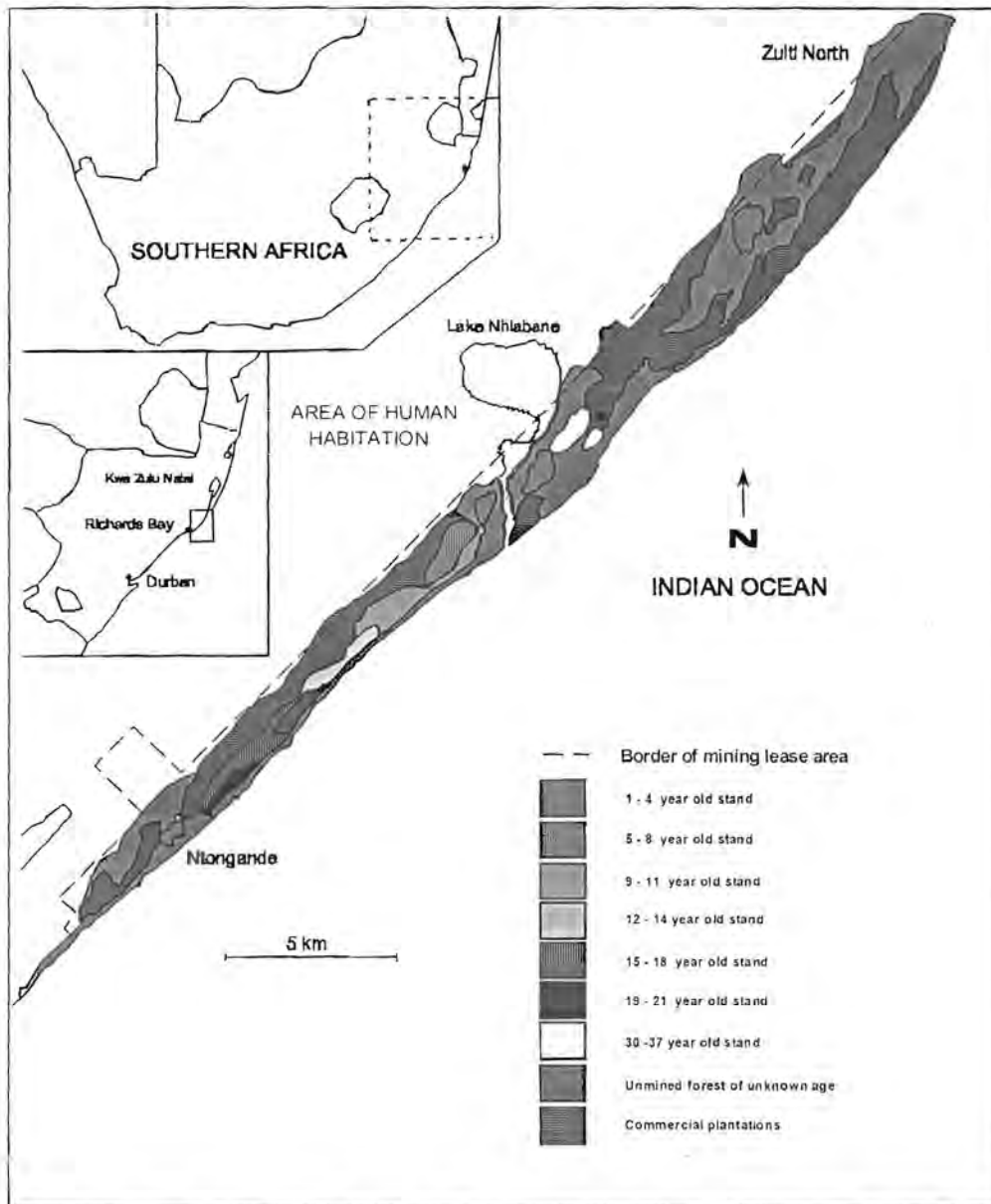


Figure 1: A map of the post-mined regenerating patches of vegetation of known age, the Zulti/Sokhulu (“bench-mark”) forest and commercial plantations. The map is based on information collected during the 1998/99 study period.

3. All measurements were accurate and without any rounding errors. This assumption prevents the heaping of data.
4. No birds were surveyed based on vocalisations. It is almost impossible to estimate densities from singing and calling birds alone. Such estimates will most certainly result in overestimated densities (Bart & Schoutz 1984).

Primary analysis

All data collected were presented in a matrix format, with rows representing the relative densities of each bird species and columns the transect lines within each of the sampled sites. This matrix formed the bases of the analyses that follow in the proceeding chapters. Relative densities (rD) were obtained using the equation $rD = rN/rV$, where rN is the relative number seen (the number of a specific species seen relative to the total number seen on the transect) and rV is relative visibility (see Buckland *et al.* 1992), calculated as the ratio of density when equal visibility is assumed (rN multiplied by total density) to estimated density (using DISTANCE). The relative densities of each species for each sampling site were standardized due to unequal sample sizes for transect lines on each sampling site. Several measures describe the similarity of species abundance between samples and in this study the Bray-Curtis similarity index or coefficient was calculated. The index describes the similarity between species *a* and *b* ($B-CS_{ab}$) and was calculated as:

$$B-CS_{ab} = \frac{2 \sum \min(x_{ca}, x_{cb})}{\sum x_{ca} \sum x_{cb}}$$

where x_{ca} and x_{cb} were fourth-root transformed parameters (abundance, relative densities or biomass) of species *a* and species *b* respectively.

All multivariate analyses were performed using the software package PRIMER v4.0 (1994). This was done by calculating Bray-Curtis similarities between every pair of samples to construct a similarity matrix. This matrix was subsequently used to discriminate between sampled sites through cluster analysis and ordination techniques (non-metric multidimensional scaling) and analysis of similarities. The importance of very abundant species had to be down-weighted in order to give some importance to low abundance or rare species. This was achieved by performing a fourth root transformation on the raw data set (Clarke & Warwick 1994). Secondary and additional analyses will be considered in the relevant chapters.

Chapter 3

Development of bird assemblages on rehabilitating coastal dune forests

Introduction

The development of biological communities is often dictated by ecological succession. Succession is the non-seasonal, directional and continuous colonisation and extinction of a specific area by species populations, and is typically initiated by disturbances (Begon *et al.* 1986). Studies on the post-mining regeneration of several coastal dune plant and animal communities in my study area confirmed that age related trends in a variety of communities, converge in similarity towards those typical of an undisturbed forest in the region (Van Aarde *et al.* 1996a, Van Aarde *et al.* 1996b, Ferreira & van Aarde 1997, Kritzinger & van Aarde 1998). Here the number of feeding guilds, species densities, and species richness for birds increased as vegetation structure became more complex through time (Kritzinger & van Aarde 1998).

Based on other studies, life history traits such as the size of an organism should increase, and selection pressures should move from r- towards K-selection (Odum 1969, Smith & MacMahon 1981) during succession. Furthermore, the reproductive output of birds typically decreases with successional progress due to the greater incidence of multiple-brooding and increasing environmental stability (May 1984, Mönkkönen & Helle 1987).

Floristic properties and plant species contribute towards habitat diversity and have been one of the most predictive variables in explaining patterns in bird species richness (Erdelen 1984, Willson 1974). Most studies infer that bird species richness is a consequence of foliage height diversity (MacArthur & MacArthur 1961, MacArthur 1964, Willson 1974, Wiens 1989, Kritzinger 1996).

The description of the regenerating bird community of my study area by Kritzinger & van Aarde (1998) focussed on variables recorded during the instantaneous sampling of a regenerating successional coastal dune sere of known age. In substituting space for time, these authors described trends in species composition, diversity, richness and density with stand age and compared these

variables with trends recorded on a nearby unmined coastal dune forest. They formulated two hypotheses - the first states that bird species that both diversity and richness as well total density increase with habitat regeneration age.

Here I repeat their analysis, documenting age related trends in community variables for two study periods (1993/94 and 1998/99). This provides an opportunity to challenge the assumption of Kritzinger & van Aarde (1998) that development of the communities on each of the known aged seral stages would follow the same pathway. In this part of my study I compare age related changes in species composition, species richness and species diversity of the bird community as reflected during two study bouts five years apart.

Material and Methods

The collection of relevant information has been described in Chapter 2. Sampling took place during the austral winters (1 July to 29 August) and summers (1 December to 22 December) of 1993/94 and 1998/99. Data used in this chapter include those collected from six known-age, post-mined regenerating sites, from an unmined mature dune forest (Zulti/Sokhulu) and from a 32-37 year old site of indigenous vegetation (see Chapter 2). Unless otherwise stated, all data were analysed for each study site (see Chapter 2 for a description of each of the sites), through both study periods, during both summer and winter seasons.

Macro-parameters (abundance and diversity patterns)

Relative densities were calculated for each species, though data for seasons were pooled. Analyses for the 1993/94 study period are based on the information collected by Kritzinger 1996 and Kritzinger & van Aarde (1998). A full description of the methods followed to determine density for each sampling site is presented in Chapter 2.

The mean number of species, total density (density for all species ha^{-1}) per sampling site, species richness (S), Shannon diversity index (H') and Pielou's evenness index (E) were calculated for each study period (H' and E are described by Magurran (1988)). Statistical differences between the means for the study periods were determined using Kruskal-Wallis one-way analyses of ranks and Dunn's

distribution free multiple range test (Sokal & Rohlf 1995). These non-parametric tests were used as the variables under consideration for each sampling site were not normally distributed.

Differences in log-transformed species richness (S), Shannon diversity index (H') and Pielou's evenness index (E) were investigated through least square regression analyses for each study period, in relationship to the median age of the sampling sites.

Rarefaction was used to calculate the expected number of species ($E[S_n]$) in a random sample of n individuals less than the original sample of N individuals. This was done for all species without any replacement of individuals (James & Wamer

1982) using the following equation: $[E(S_n)] = \sum (1 - \frac{\binom{N-n}{i}}{\binom{N}{i}})$, where N_i refers to the

number of individuals of i species seen (James & Rathbun 1981).

Rank-abundance curves were constructed for each sampling site as described by Tokeshi (1993), by plotting the relative densities of each species against species ranks. Least square regression analyses of log-transformed relative densities were used to fit the curves and enable the comparison of slopes between the different sampling sites for equitability (Tokeshi 1993).

Community composition

A comparison of the different sites was conducted based on relative densities using Bray-Curtis similarity coefficients, while multivariate community analyses were performed using PRIMER v4.0 (1994). Both of these procedures are described in Chapter 2. The relative densities of each species were standardised to percentage values due to the unequal number of transect lines on different sampling sites. Similarity matrices of transformed data were exposed to cluster analyses based on hierarchical agglomerative clustering with group-average linking, as described by Clarke & Warwick (1994).

Non-metric multidimensional scaling (MDS)¹ was used to map inter-relationships between sampling sites in an ordination with a specified number of

¹ A MDS has an advantage over other ordination techniques (PCA and correspondence analysis) in as far as its flexibility and lack of assumptions (Field *et al.* 1982, Kenkel & Orloci 1986, Clarke 1993). Data with lots of zero's which lack the assumptions of normality can be used when transformed. A MDS has good distance preservation properties and therefore a 2-dimensional plot is a method to minimize stress values (Field *et al.* 1982).

dimensions (Kruskal & Wish 1978, Clarke 1993). MDS was performed for each transect line within a sampling site. Any significant differences between community structure for the sampling sites were more closely tested using the program ANOSIM² (analysis of similarity). These tests were performed on the similarity matrix calculated for both study periods for each season (Clarke & Green 1988).

The program SIMPER (similarity percentage) (PRIMER v4.0, 1994) was used to determine the contribution (%) of each species to each sampling site, as well as the consistency of each species contribution to similarity between sites for a given study period (Clarke & Warwick 1994). The species with the highest consistency were considered as typical species for a given assemblage. The same program was used to measure the dissimilarity between sampling sites within a study period. Therefore, species that contributed most to the dissimilarity between two successional stages of development were considered as good discriminant species. As such, discriminant species will occur in one of the assemblages of a sampling site but be absent or in low abundance in the other sites.

Results

Macro-parameters (abundance and diversity patterns)

Relative densities of species during both study periods

During both study periods and for each of the seasons, increased regeneration age was associated with an increase in the number of species recorded (see Tables 4, 5 & 6). Species occurring at relatively high densities during early vegetation development (1-4 year old site) tended to decrease in abundances with increased regeneration age (5-8 year old site).

² This is a permutation procedure to the rank similarity matrix of the specified ordination (Clarke & Green 1988). It uses the Global R test statistic as a degree of difference between groups or clusters and the value thereof falls between 0 and 1. R = 1 indicate that samples within a cluster are more similar to each other than samples in other clusters, and R = 0 when samples between clusters are more similar. If R is significantly from zero, then there are significant differences between clusters within the similarity matrix (Clarke & Green 1988).

Table 4: The mean \pm S. E. relative densities of each species for each sampling site during two study periods (seasons pooled). Weavers[†] refers to mixed flocks of Yellow and Lesser Masked Weavers.

Species	Sampling site							
	1-4 years		5-8 years		9-11 years		12-14 years	
	1993/94	1998/99	1993/94	1998/99	1993/94	1998/99	1993/94	1998/99
Blackeyed Bulbul					0.060 \pm 0.013	0.016 \pm 0.009	0.063 \pm 0.014	0.055 \pm 0.011
Bleating Warbler			0.007 \pm 0.005	0.400 \pm 0.137	0.256 \pm 0.076	0.455 \pm 0.037	0.155 \pm 0.057	0.203 \pm 0.019
Bluegrey Flycatcher							0.051 \pm 0.017	Not recorded
Bronze Mannikin	0.168 \pm n/a	Not recorded						
Cape White-eye							0.009 \pm 0.009	0.069 \pm 0.016
Common Waxbill	0.020 \pm n/a	0.349 \pm 0.146						
Fantailed Cisticola	0.409 \pm n/a	0.140 \pm 0.029						
Forest Weaver					Not recorded	0.081 \pm 0.031		
Grassveld Pipit	0.060 \pm n/a	0.025 \pm 0.017						
Lesser Masked Weaver			0.008 \pm 0.004	0.059 \pm 0.028	0.139 \pm 0.059	0.183 \pm 0.033		
Natal Robin			Not recorded	0.085 \pm 0.046			0.010 \pm 0.010	0.063 \pm 0.023
Pallid Flycatcher							0.100 \pm 0.013	Not recorded
Rudd's Apalis			Not recorded	0.106 \pm 0.045	0.002 \pm 0.002	0.098 \pm 0.024		
Rattling Cisticola	0.013 \pm n/a	0.219 \pm 0.117	0.469 \pm 0.106	0.181 \pm 0.058	0.246 \pm 0.090	Not recorded		
Sombre Bulbul							Not recorded	0.059 \pm 0.018
Tawnyflanked Prinia	0.009 \pm n/a	0.080 \pm 0.040	0.029 \pm 0.012	0.019 \pm 0.037	0.148 \pm 0.017	0.069 \pm 0.017		
Weavers [†]	0.050 \pm n/a	Not recorded	0.053 \pm 0.027	Not recorded	0.125 \pm 0.016	Not recorded		
Whitebrowed Robin			0.007 \pm 0.005	0.059 \pm 0.019	0.047 \pm 0.021	0.074 \pm 0.013		
Willow Warbler					0.087 \pm 0.075	Not recorded		
Yellowbreasted Apalis			0.040 \pm 0.010	0.123 \pm 0.055	0.233 \pm 0.097	0.265 \pm 0.048	0.295 \pm 0.089	0.300 \pm 0.035
Yellowbellied Bulbul					0.013 \pm 0.009	0.070 \pm 0.025	0.067 \pm 0.049	0.069 \pm 0.014
Yellow Weaver	0.008 \pm n/a	0.133 \pm 0.063	0.258 \pm 0.046	0.114 \pm 0.065	0.059 \pm 0.023	0.114 \pm 0.041	0.018 \pm 0.016	0.104 \pm 0.091

(Table 4 continue)

Species	Sampling site							
	15-18 years		19-21 years		32-37 years		Mature	
	93/94	98/99	93/94	98/99	93/94	98/99	93/94	98/99
Blackeyed Bulbul					0.030 ± n/a	0.056 ± 0.021		0.050 ± 0.009
Bleating Warbler	0.159 ± 0.046	0.170 ± 0.035		0.281 ± 0.016	0.110 ± n/a	0.181 ± 0.031		0.188 ± 0.022
Bluegrey Flycatcher	0.054 ± 0.028	0.013 ± 0.010						
Bronze Mannikin								
Cape White-eye	0.051 ± 0.024	0.043 ± 0.018		0.180 ± 0.069	0.359 ± n/a	0.116 ± 0.053		0.052 ± 0.021
Collared Sunbird				0.073 ± 0.017	0.090 ± n/a	0.042 ± 0.018		
Common Waxbill								
Fantailed Cisticola								
Forest Weaver								
Goldenrumped Tinker Barbet					0.057 ± n/a	0.033 ± 0.008		
Grassveld Pipit								
Lesser Masked Weaver	0.011 ± 0.006	0.249 ± 0.055						
Natal Robin				0.075 ± 0.018	0.037 ± n/a	0.061 ± 0.021		0.063 ± 0.011
Olive Sunbird					0.050 ± n/a	0.138 ± 0.029		0.102 ± 0.028
Pallid Flycatcher								
Puffback	0.054 ± 0.018	0.021 ± 0.003		0.052 ± 0.012				0.058 ± 0.012
Rudd's Apalis								
Rattling Cisticola								
Sombre Bulbul					0.016 ± n/a	0.203 ± 0.032		0.092 ± 0.021
Southern Boubou					0.004 ± n/a	0.060 ± 0.036		
Squaretailed Drongo	0.055 ± 0.020	0.037 ± 0.011						
Tawnyflanked Prinia								
Terrestrial Bulbul Weavers ⁵								0.097 ± 0.026
Whitebrowed Robin								
Willow Warbler								
Yellowbreasted Apalis	0.384 ± 0.022	0.118 ± 0.024		0.220 ± 0.022	0.239 ± n/a	0.058 ± 0.025		0.081 ± 0.018
Yellowbellied Bulbul	0.038 ± 0.017	0.069 ± 0.033		0.087 ± 0.022	0.169 ± n/a	0.097 ± 0.032		0.176 ± 0.026
Yellow Weaver	0.017 ± 0.017	0.061 ± 0.034						

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Table 5: The mean \pm S. E. relative densities of each species for each sampling site during the summers of 1993/94 and 1998/99. Weavers[†] refers to mixed flocks of Yellow and Lesser Masked Weavers.

Species	Sampling Site							
	1-4 years		5-8 years		9-11 years		12-14 years	
	93/94	98/99	93/94	98/99	93/94	98/99	93/94	98/99
Blackeyed Bulbul	0.045 \pm n/a	0.068 \pm 0.043					0.098 \pm 0.005	0.021 \pm 0.013
Bleating Warbler			Not recorded	0.376 \pm 0.148	0.280 \pm 0.076	0.541 \pm 0.043	0.175 \pm 0.096	0.267 \pm 0.026
Bluegrey Flycatcher							0.093 \pm 0.025	Not recorded
Cape White-eye							0.019 \pm 0.019	0.105 \pm 0.036
Fantailed Cisticola	0.613 \pm n/a	0.018 \pm 0.012						
Forest Weaver					Not recorded	0.124 \pm 0.051		
Grassveld Pipit	0.067 \pm n/a	Not recorded						
Lesser Masked Weaver					0.100 \pm 0.100	0.254 \pm 0.078		
Olive Sunbird							0.056 \pm 0.032	0.028 \pm 0.017
Puffback							0.031 \pm 0.002	0.051 \pm 0.025
Rudd's Apalis			Not recorded	0.097 \pm 0.038	Not recorded	0.125 \pm 0.046		
Rattling Cisticola	0.026 \pm n/a	0.341 \pm 0.164	0.650 \pm 0.146	0.196 \pm 0.069	0.173 \pm 0.060	Not recorded		
Tawnyflanked Prinia	Not recorded	0.134 \pm 0.074	0.036 \pm 0.012	0.165 \pm 0.030	0.149 \pm 0.049	0.092 \pm 0.044		
Weavers [†]	0.083 \pm n/a	Not recorded	0.079 \pm 0.051	Not recorded	0.089 \pm 0.045	Not recorded	0.061 \pm 0.061	Not recorded
Whitebrowed Robin			0.009 \pm 0.009	0.102 \pm 0.030	0.079 \pm 0.040	0.055 \pm 0.027		
Willow Warbler					0.173 \pm 0.150	Not recorded	0.059 \pm 0.040	Not recorded
Yellowbreasted Apalis			0.060 \pm 0.009	0.141 \pm 0.062	0.348 \pm 0.151	0.241 \pm 0.095	0.341 \pm 0.099	0.376 \pm 0.056
Yellowbellied Bulbul					0.013 \pm 0.013	0.079 \pm 0.027	0.119 \pm 0.104	0.094 \pm 0.025
Yellow Weaver	0.015 \pm n/a	0.266 \pm 0.126	0.127 \pm 0.048	0.184 \pm 0.105	0.081 \pm 0.042	0.055 \pm 0.038	0.033 \pm 0.033	0.056 \pm 0.056

(Table 5 continue)

Species	Sampling Site							
	15-18 years		19-21 years		32-37 years		Mature	
	93/94	98/99	93/94	98/99	93/94	98/99	93/94	98/99
Blackeyed Bulbul	0.047 ± 0.011	0.050 ± 0.025			0.046 ± n/a	0.055 ± 0.034		0.079 ± 0.018
Bleating Warbler	0.169 ± 0.045	0.240 ± 0.059		0.298 ± 0.044	0.178 ± n/a	0.198 ± 0.054		0.135 ± 0.030
Bluegrey Flycatcher	0.108 ± 0.056	0.022 ± 0.022						
Cape White-eye	0.051 ± 0.006	0.059 ± 0.032		0.166 ± 0.034	0.193 ± n/a	0.124 ± 0.071		
Collared Sunbird	0.069 ± 0.042	0.017 ± 0.011		0.051 ± 0.018	0.157 ± n/a	0.058 ± 0.026		
Forest Weaver	0.058 ± 0.014	0.045 ± 0.021			0.070 ± n/a	0.024 ± 0.021		
Grey Sunbird	0.056 ± 0.056	Not recorded						
Natal Robin				0.051 ± 0.030	Not recorded	0.088 ± 0.031		0.088 ± 0.015
Olive Sunbird					0.078 ± n/a	0.181 ± 0.051		0.087 ± 0.026
Puffback				0.051 ± 0.022				0.075 ± 0.023
Southern Boubou					Not recorded	0.071 ± 0.029		
Squaretailed Drongo	0.072 ± 0.038	0.058 ± 0.027						
Terrestrial Bulbul								0.135 ± 0.036
Wattle-eyed Flycatcher								0.050 ± 0.025
Yellowbreasted Apalis	0.295 ± 0.061	0.129 ± 0.023		0.187 ± 0.032	0.339 ± n/a	0.094 ± 0.036		0.095 ± 0.023
Yellowbellied Bulbul	0.069 ± 0.028	0.068 ± 0.036		0.103 ± 0.044	0.240 ± n/a	0.089 ± 0.038		0.215 ± 0.050
Yellow Weaver	0.035 ± 0.035	0.076 ± 0.060						

Table 6: The mean \pm S. E. relative densities of each species for each sampling site during the winters of 1993/94 and 1998/99. Weavers[†] refers to mixed flocks of Yellow and Lesser Masked Weavers.

Species	Sampling Site							
	1-4 years		5-8 years		9-11 years		12-14 years	
	93/94	98/99	93/94	98/99	93/94	98/99	93/94	98/99
Blackeyed Bulbul					0.095 \pm 0.047	0.031 \pm 0.018	0.029 \pm 0.023	0.090 \pm 0.029
Bleating Warbler			0.014 \pm 0.010	0.425 \pm 0.127	0.232 \pm 0.078	0.368 \pm 0.048	0.135 \pm 0.076	0.140 \pm 0.051
Bronze Mannikin	0.337 \pm n/a	Not recorded						
Common Waxbill	Not recorded	0.691 \pm 0.293						
Fantailed Cisticola	0.205 \pm n/a	0.263 \pm 0.053						
Grassveld Pipit	0.065 \pm n/a	0.050 \pm 0.035						
Grey Waxbill			Not recorded	0.053 \pm 0.053				
Hadedda Ibis							0.013 \pm 0.013	0.095 \pm 0.095
Lesser Masked Weaver			0.015 \pm 0.008	0.106 \pm 0.057	0.177 \pm 0.052	0.113 \pm 0.054	0.058 \pm 0.038	0.013 \pm 0.013
Natal Robin			Not recorded	0.170 \pm 0.092			0.020 \pm 0.020	0.121 \pm 0.042
Pallid Flucatcher							0.200 \pm 0.026	Not recorded
Rudd's Apalis			Not recorded	0.116 \pm 0.065	0.003 \pm 0.003	0.071 \pm 0.027		
Rattling Cisticola	Not recorded	0.097 \pm 0.069	0.288 \pm 0.075	0.167 \pm 0.059	0.319 \pm 0.143	Not recorded		
Sombre Bulbul			Not recorded	0.072 \pm 0.039			Not recorded	0.118 \pm 0.035
Tawnyflanked Prinia			0.022 \pm 0.012	0.215 \pm 0.053	0.147 \pm 0.014	0.046 \pm 0.027		
Weavers [†]					0.162 \pm 0.077	Not recorded		
Whitebrowed Robin					0.015 \pm 0.009	0.094 \pm 0.016		
Yellowbreasted Apalis			0.020 \pm 0.013	0.105 \pm 0.062	0.118 \pm 0.048	0.289 \pm 0.080	0.248 \pm 0.088	0.224 \pm 0.063
Yellowbellied Bulbul					0.013 \pm 0.007	0.062 \pm 0.029		
Yelloweyed Canary					0.075 \pm 0.048	Not recorded		
Yellow Weaver			0.390 \pm 0.102	0.045 \pm 0.031	0.037 \pm 0.017	0.173 \pm 0.055	0.003 \pm 0.003	0.151 \pm 0.127

(Table 6 continue)

Species	Sampling Site							
	15-18 years		19-21 years		32-37 years		Mature	
	93/94	98/99	93/94	98/99	93/94	98/99	93/94	98/99
Black-eyed Bulbul					0.013 ± n/a	0.056 ± 0.023		
Bleating Warbler	0.150 ± 0.077	0.100 ± 0.035		0.264 ± 0.063	0.041 ± n/a	0.164 ± 0.035		0.241 ± 0.040
Bluegrey Flycatcher								
Cape White-eye	0.050 ± 0.042	0.027 ± 0.019		0.193 ± 0.122	0.524 ± n/a	0.108 ± 0.045		0.066 ± 0.027
Collared Sunbird				0.095 ± 0.029				0.050 ± 0.015
Dusky Flycatcher					0.094 ± n/a	0.025 ± 0.016		
Forest Weaver								0.058 ± 0.030
Golden-rumped Tinker Barbet					0.065 ± n/a	0.024 ± 0.010		
Green Twinspot	0.085 ± 0.085	0.043 ± 0.008						
Grey Sunbird								
Lesser Masked Weaver	0.013 ± 0.013	0.458 ± 0.135			Not recorded	0.051 ± 0.051		
Natal Robin				0.100 ± 0.023	0.075 ± n/a	0.034 ± 0.024		
Olive Sunbird					0.021 ± n/a	0.096 ± 0.030		0.117 ± 0.033
Pallid Flycatcher	0.066 ± 0.057	Not recorded						
Puffback	0.062 ± 0.020	Not recorded		0.053 ± 0.012				
Red-eyed Dove					0.026 ± n/a	0.054 ± 0.031		
Sombre Bulbul				0.050 ± 0.017	0.033 ± n/a	0.399 ± 0.065		0.166 ± 0.042
Southern Boubou								
Square-tailed Drongo								
Terrestrial Bulbul								0.060 ± 0.032
Wattle-eyed Flycatcher								
Yellowbreasted Apalis	0.472 ± 0.078	0.108 ± 0.032		0.253 ± 0.048	0.139 ± n/a	0.023 ± 0.014		0.066 ± 0.026
Yellowbellied Bulbul	0.007 ± 0.007	0.070 ± 0.044		0.071 ± 0.024	0.098 ± n/a	0.105 ± 0.069		0.138 ± 0.015
Yellow Weaver								

Fantailed Cisticola *Cisticola juncidis*, Rattling Cisticola *C. chiniana*, Bleating Warbler *Camaroptera brachyura*, Yellowbreasted Apalis *Apalis flavida* and Cape White-eye *Zosterops pallidus* dominated during the 1993/94 study period (Table 4, Fig. 2). However, during the 1998/99 study period, Common Waxbill *Estrilda astrild*, Rattling Cisticola, Bleating Warbler, Yellowbreasted Apalis, Lesser Masked Weaver *Ploceus intermedius*, Cape White-eye, Olive Sunbird *Nectarinia olivacea* and Yellowbellied Bulbul *Chlorocichla flaviventris* dominated (Table 4, Fig. 2).

Relative densities during the summer (1993/94)

The 1-4 year old regenerating site, which constituted a grassland habitat, was dominated by Fantailed Cisticola (relative density >0.5). As habitat regeneration age increased, shrublands (5-8 year old regenerating vegetation) were colonised by Rattling Cisticola (relative density >0.5). Yellowbreasted Apalis (relative density >0.3) colonised the 9-11 year old regenerating vegetation, at an age when the relative densities of Rattling Cisticolas dropped (see Table 5). The 12-14 year old study site accommodated several more dominant species including Bleating Warbler and Yellowbreasted Apalis (relative densities > 0.15). The 15-18 years old study site was dominated by Yellowbreasted Apalis (relative densities > 0.3), whereas the 32-37 year old study site was dominated by Yellowbreasted Apalis and Yellowbellied Bulbul (relative densities >0.2).

Relative densities during the winter (1993/94)

Grasslands were dominated by Bronze Mannikin *Spermestes cucullatus*, while shrublands on the 5-8 year old site were mostly inhabited by Yellow Weaver *Ploceus subaureus*, with a relative density >0.35. Rattling Cisticola dominated (relative densities >0.3) on the 9-11 year old site. On the 12-14 years old site the Yellowbreasted Apalis persisted as the dominant species with the addition of Pallid Flycatcher *Melaenornis pallidus* (see Table 6). The 15-18 year old site was also dominated by Yellowbreasted Apalis (relative densities > 0.3), whereas the 32-37 year old site was dominated by Cape White-eye (relative densities >0.5). There was a marked decline in relative densities during the winter (see Table 6) when compared to relative densities of species during the summer (see Table 5).

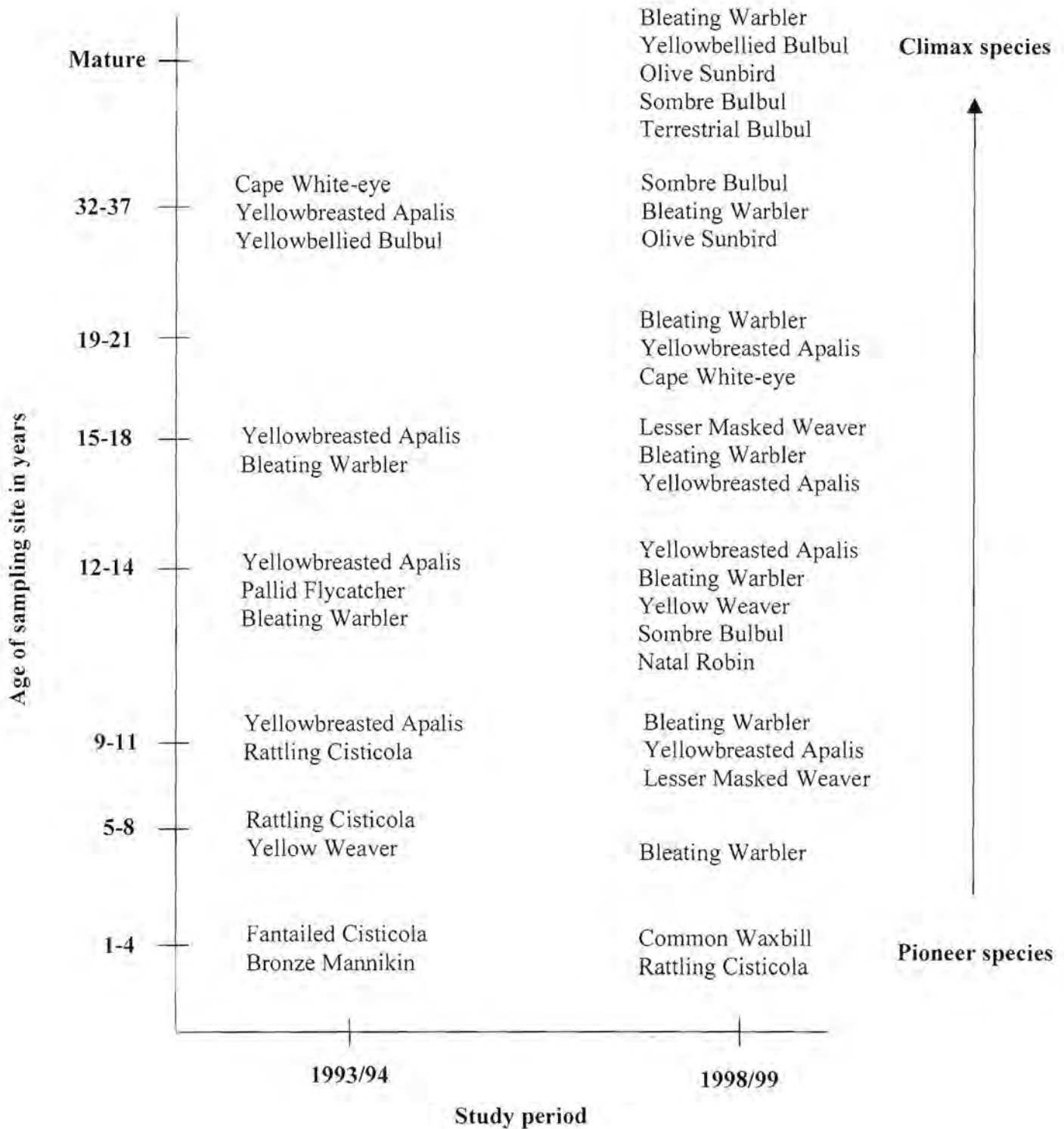


Figure 2: The dominant bird species in each sampling site for the 1993/94 and 1998/99 study periods. The species are arranged in a decreasing order of relative densities (see Table 4 for values on relative densities).

Relative densities during the summer (1998/99)

The species composition in the grasslands (1-4 year old site) was dominated by Rattling Cisticola (relative density >0.25) (Table 5). The 5-8 year old site was dominated by Bleating Warbler (relative densities >0.25), the 9-11, 12-14 and 15-18 year old sites all by Bleating Warbler and Yellowbreasted Apalis and the 19-21 year old study site by the species Bleating Warbler (relative density of 0.3). Species that dominated the 32-37 year old assemblage included Olive Sunbird and Bleating Warbler, with relative densities of up to 0.2. The unmined forest harboured mostly species such as Bleating Warbler and Yellowbellied Bulbul (see Table 5).

Relative densities during the winter (1998/99)

The dominant species on the grasslands shifted from the Rattling Cisticola to Common Waxbill (relative density >0.5). As regeneration age progressed, more species exhibited higher relative densities during the winter than during the summer, a different pattern to that observed during 1993/94 (see Table 6). The 5-8 year old sites were dominated by Bleating Warbler (relative densities >0.25), the 9-11 year site by Bleating Warbler and Yellowbreasted Apalis while the Bleating Warbler, Yellowbreasted Apalis, Yellow Weaver, Sombre Bulbul *Andropadus importunus* and Natal Robin *Cossypha natalensis* dominated the 12-14 years old site at relative densities >0.1 . The 15-18 year old site was dominated by Lesser Masked Weaver occurring at a relative density of >0.4 while the 19-21 year old site was dominated by both Bleating Warbler and Yellowbreasted Apalis (relative densities >0.2). The most dominant species on the 32-37 year old site was the Sombre Bulbul with relative densities of up to 0.4. The bird assemblage of the unmined site changed little from summer to winter but harboured higher densities of Bleating Warbler and Sombre Bulbul in winter than summer (see Table 6).

Regeneration Age related trends

The mean number of species present increased with an increase in site regeneration age during both study periods, with the oldest areas harbouring the greatest number of species. Based on the statistical analyses of the slopes of the linear regression lines describing these trends, the differences for the two study periods were not significant ($F=2.46$, $p=0.15$). During 1993/94, the greatest mean number of species was recorded

on the 32-37 year old sampling site, while the lowest values were noted for the two youngest sampling sites (Table 7). During 1998/99 the unmined area was occupied by the greatest number of species while the lowest numbers were recorded for the youngest sampling sites (Table 7).

For 1998/99 the youngest assemblages exhibited both the lowest bird species diversity and evenness (values closer to zero), while inversely the oldest assemblages had both the highest diversity and evenness (values closer to one) (see Table 7). The mean number of species, mean total density ha^{-1} , Shannon diversity and Pielou's evenness for each season did not differ significantly with an increase in site age.

For all measured variables (S, H' , E), absolute values increased with an increase in regeneration age (Table 8). The regression slopes for diversity and density, but not evenness, did not differ between study periods and seasons, though the intercepts did differ significantly (Table 8). Slopes and intercepts for evenness only differed significantly during the winter (Table 8).

The values obtained through the construction of rarefaction curves confirm an increase in the number of species with an increase in habitat regeneration age during both the 1993/94 (see Table 9) and 1998/99 (see Table 9) study periods and across both seasons (Fig. 3). The expected number of species was slightly higher for 1993/94 (more pronounced during the winter) than 1998/99.

The slopes of the rank-abundance curves for the sampling sites differed significantly from each other within a particular sampling period (1993/94_(summer): $F=17.92$, $p<0.0001$; 1993/94_(winter): $F=31.19$, $p<0.0001$ and 1998/99_(summer): $F=39.36$, $p<0.0001$; 1998/99_(winter): $F=18.10$, $p<0.0001$). These slopes also deviated significantly from zero ($p<0.001$) (Fig. 4) and decreased with an increase in regeneration age (Fig. 5). During 1993/94 the slopes decreased at the 5-8 year old site and then increased at sites aged 9-11 and 12-14 years old, while those of the 1998/99 period increased at the 5-8 year old site and then decreased at sites aged 9-11 and 12-14 years old (Fig. 5).

Community composition

The Bray-Curtis similarity coefficient, reflecting similarity in the community compositions of a specific site and that of the "bench-mark" site (here the mature dune forest), increased with an increase in habitat regeneration age during both study periods (Fig 6). Multidimensional scaling of relative densities for 1993/94 suggested

Table 7: The number of species (mean \pm S.E.), total density ha^{-1} (mean \pm S.E.), Shannon diversity (mean \pm S.E.), and Pielou's evenness (mean \pm S.E.) on each sampling site during two different study periods. Data for summers and winters were pooled. Values in brackets presents the number of transects that were surveyed. The Kruskal-Wallis test statistic is represented by H – values and test for differences between sampling sites within a study year at $p < 0.05$. Superscripts with different alphabetic letters associated with mean values donate statistical significance between sites within the same year.

Regeneration age (years)	Mean \pm S.E. number of species		Mean \pm S.E. total density ha^{-1}	
	1993/94*	1998/99	1993/94*	1998/99
	$H = 9.55, p < 0.05$	$H = 24.61, p < 0.001$	$H = 8.35, p > 0.05$	$H = 16.75, p < 0.05$
1-4	$11.50 \pm \text{n/a}$ (1) ^a	7.33 ± 0.88 (3) ^a	$33.86 \pm \text{n/a}$ (1)	14.21 ± 2.18 (3) ^a
5-8	10.17 ± 0.60 (3) ^d	10.38 ± 0.69 (4) ^a	40.36 ± 5.12 (3)	52.92 ± 11.17 (4) ^b
9-11	14.33 ± 1.45 (3) ^b	10.50 ± 0.46 (4) ^a	86.33 ± 3.47 (3)	44.28 ± 2.73 (4) ^b
12-14	14.67 ± 1.48 (3) ^b	11.00 ± 0.20 (4) ^a	39.84 ± 6.19 (3)	33.38 ± 6.76 (4) ^b
15-18	14.83 ± 0.88 (3) ^b	14.38 ± 0.72 (4) ^b	39.98 ± 11.71 (3)	31.17 ± 4.77 (4) ^b
19-21	No data	12.38 ± 1.11 (4) ^b	No data	37.48 ± 2.73 (4) ^b
32-37	$20.00 \pm \text{n/a}$ (1) ^c	15.13 ± 1.85 (4) ^c	$73.79 \pm \text{n/a}$ (1)	38.25 ± 5.88 (4) ^b
Mature	No data	16.31 ± 0.78 (8) ^c	No data	52.87 ± 5.15 (8) ^c

Regeneration age (years)	Shannon Diversity (I)		Pielou's Evenness (E)	
	1993/94*	1998/99	1993/94*	1998/99
	$H = 10.26, p > 0.05$	$H = 25.82, p < 0.001$	$H = 10.18, p > 0.05$	$H = 21.55, p < 0.01$
1-4	$1.48 \pm \text{n/a}$ (1)	1.57 ± 0.19 (3) ^a	$0.61 \pm \text{n/a}$ (1)	0.79 ± 0.05 (3) ^a
5-8	1.29 ± 0.06 (3)	2.03 ± 0.12 (4) ^{ab}	0.56 ± 0.02 (3)	0.88 ± 0.03 (4) ^{ab}
9-11	2.16 ± 0.06 (3)	2.02 ± 0.06 (4) ^{ab}	0.82 ± 0.01 (3)	0.87 ± 0.01 (4) ^{ab}
12-14	2.20 ± 0.10 (3)	2.03 ± 0.03 (4) ^{ab}	0.83 ± 0.02 (3)	0.85 ± 0.01 (4) ^{ab}
15-18	2.28 ± 0.01 (3)	2.24 ± 0.03 (4) ^{bc}	0.85 ± 0.02 (3)	0.85 ± 0.01 (4) ^{ab}
19-21	No data	2.22 ± 0.10 (4) ^{bc}	No data	0.89 ± 0.01 (4) ^{ab}
32-37	$2.39 \pm \text{n/a}$ (1)	2.42 ± 0.14 (4) ^c	$0.80 \pm \text{n/a}$ (1)	0.90 ± 0.01 (4) ^{bc}
Mature	No data	2.58 ± 0.06 (8) ^c	No data	0.93 ± 0.01 (8) ^c

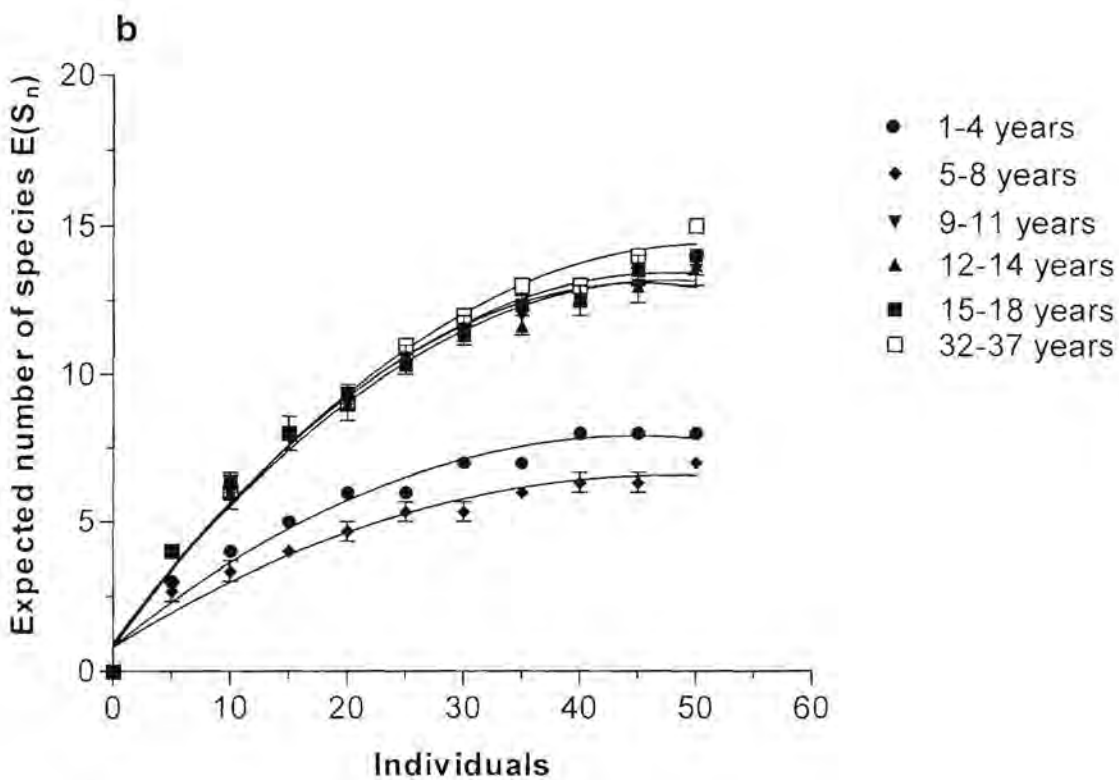
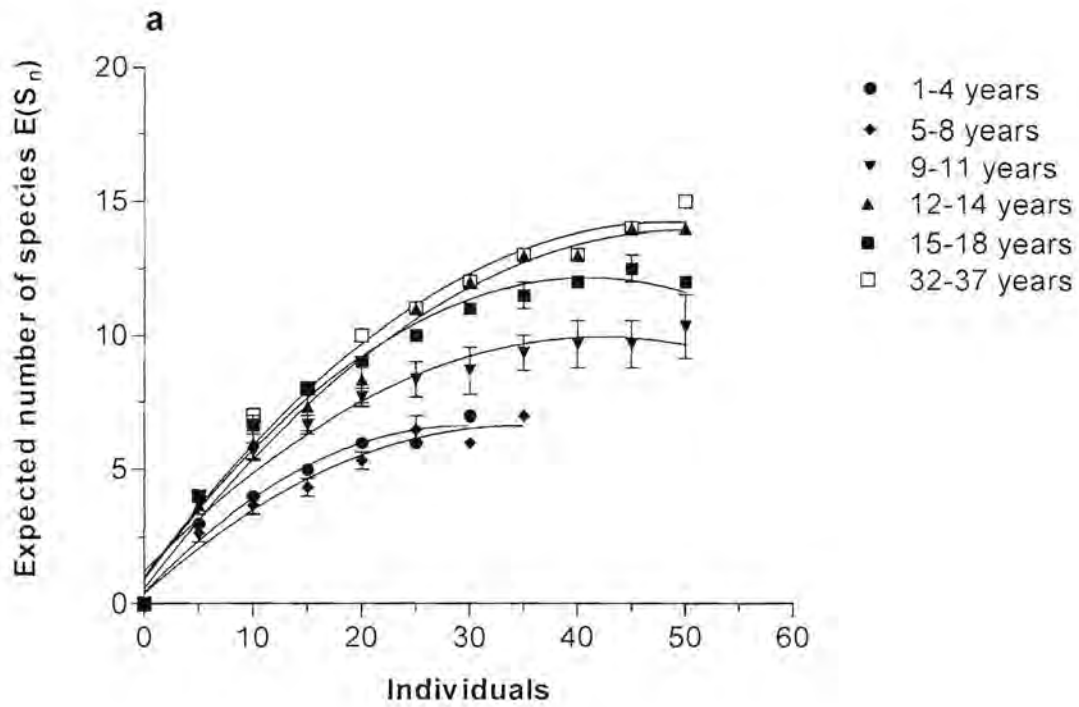
* Raw data from archives of RJ van Aarde and collected as described by Kritzing & van Aarde (1998)

Table 8: Least square linear regression variables and associated statistical values to express log-transformed Shannon diversity, evenness and species richness variables as a function of the regeneration. $p < 0.05$ = significant differences between slopes and intercepts.

Variable and parameter	Study period		Comparison between slopes of 1993/94 and 1998/99		Comparison between intercepts of 1993/94 and 1998/99		
	1993/94	1998/99	F-ratio	p-value	F-ratio	p-value	
Shannon diversity	Summer						
	Y = a + bX	Y=2.03+0.02X	Y=1.92+0.02X				
	F-ratio	49.26	29.01				
	R ²	0.92	0.83				
	p-value	0.002	0.001				
				0.30	0.59	5.33	0.04
	Winter						
	Y = a + bX	Y=2.36+0.02X	Y=2.25+0.01X				
F-ratio	7.30	5.50					
R ²	0.68	0.48					
p-value	0.05	0.06					
			1.34	0.27	6.76	0.02	
Evenness	Summer						
	Y = a + bX	Y=0.94+0.001X	Y=0.95+0.001X				
	F-ratio	1.39	5.90				
	R ²	0.26	0.50				
	p-value	0.30	0.05				
				0.07	0.80	0.87	0.37
	Winter						
	Y = a + bX	Y=0.93+0.001X	Y=0.96+0.001X				
F-ratio	7.23	40.84					
R ²	0.64	0.87					
p-value	0.05	0.001					
			5.87	0.03	-	-	
Species richness	Summer						
	Y = a + bX	Y=8.21+0.31X	Y=7.27+0.23X				
	F-ratio	179.6	62.86				
	R ²	0.98	0.91				
	p-value	0.0002	0.0002				
				3.16	0.11	12.60	0.01
	Winter						
	Y = a + bX	Y=12.75+0.25X	Y=10.85+0.10X				
F-ratio	8.43	5.17					
R ²	0.68	0.46					
p-value	0.04	0.06					
			2.46	0.15	12.05	0.01	

Table 9: The mean \pm S.E. expected number of species for each sampling site based on rarefaction curves (see Fig. 3).

Regeneration age in years	Study period 1993/94						Study period 1998/99					
	Summer			Winter			Summer			Winter		
	Expected number of species	Number of individuals	R ²	Expected number of species	Number of individuals	R ²	Expected number of species	Number of individuals	R ²	Expected Number of species	Number of individuals	R ²
1-4	7.0 \pm n/a	30.0 \pm n/a	0.97	8.0 \pm n/a	50.0 \pm n/a	0.97	5.7 \pm 3.2	18.3 \pm 11.6	0.95	7.3 \pm 1.5	31.7 \pm 5.8	0.83
5-8	6.3 \pm 1.2	25.0 \pm 5.0	0.93	7.0 \pm 0.0	50.0 \pm 0.0	0.92	8.25 \pm 1.5	22.5 \pm 5.0	0.91	9.5 \pm 2.6	22.5 \pm 2.9	0.91
9-11	10.3 \pm 2.1	50.0 \pm 0.0	0.86	11.7 \pm 3.2	40.0 \pm 17.3	0.97	7.5 \pm 1.3	18.8 \pm 2.5	0.95	10.3 \pm 1.7	23.8 \pm 2.5	0.95
12-14	9.7 \pm 3.8	30.0 \pm 17.3	0.96	13.7 \pm 0.6	50.0 \pm 0.0	0.98	7.3 \pm 1.7	18.8 \pm 6.3	0.97	10.5 \pm 1.9	25.0 \pm 4.1	0.93
15-18	11.7 \pm 1.5	38.3 \pm 16.1	0.97	13.7 \pm 0.6	45.0 \pm 8.7	0.97	11.0 \pm 0.8	26.3 \pm 2.5	0.98	12.5 \pm 2.1	33.8 \pm 10.3	0.97
19-21	-	-	-	-	-	-	10.5 \pm 2.5	25.0 \pm 4.1	0.91	11.3 \pm 2.9	33.8 \pm 7.5	0.88
32-37	15.0 \pm n/a	50.0 \pm n/a	0.98	15.0 \pm n/a	50.0 \pm n/a	0.99	14.0 \pm 3.2	28.8 \pm 6.3	0.95	12.3 \pm 4.1	26.3 \pm 8.5	0.97
Mature	-	-	-	-	-	-	15.8 \pm 3.4	31.3 \pm 11.3	0.98	13.8 \pm 2.5	31.9 \pm 6.5	0.95



(Fig. 3. continue)

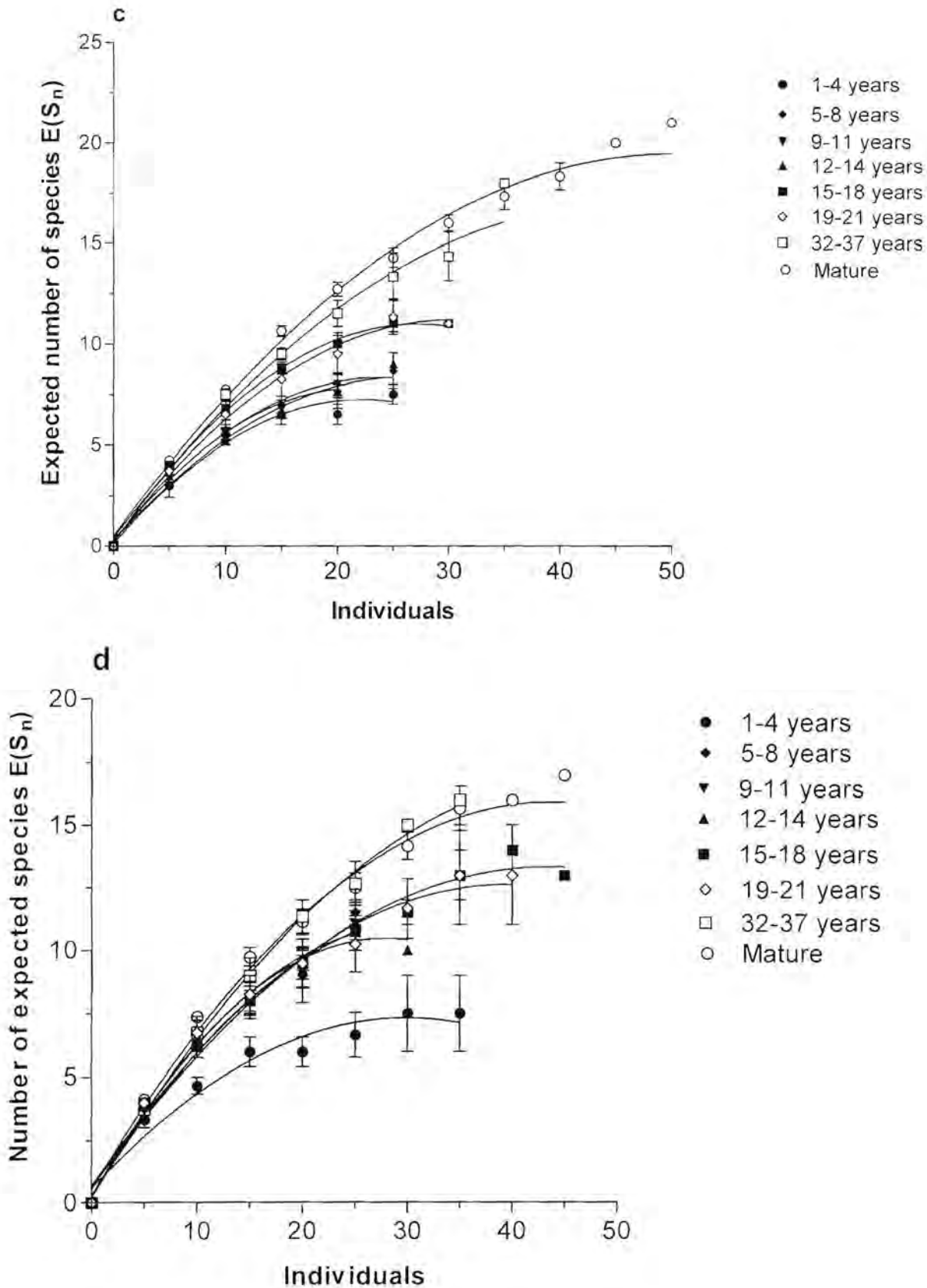
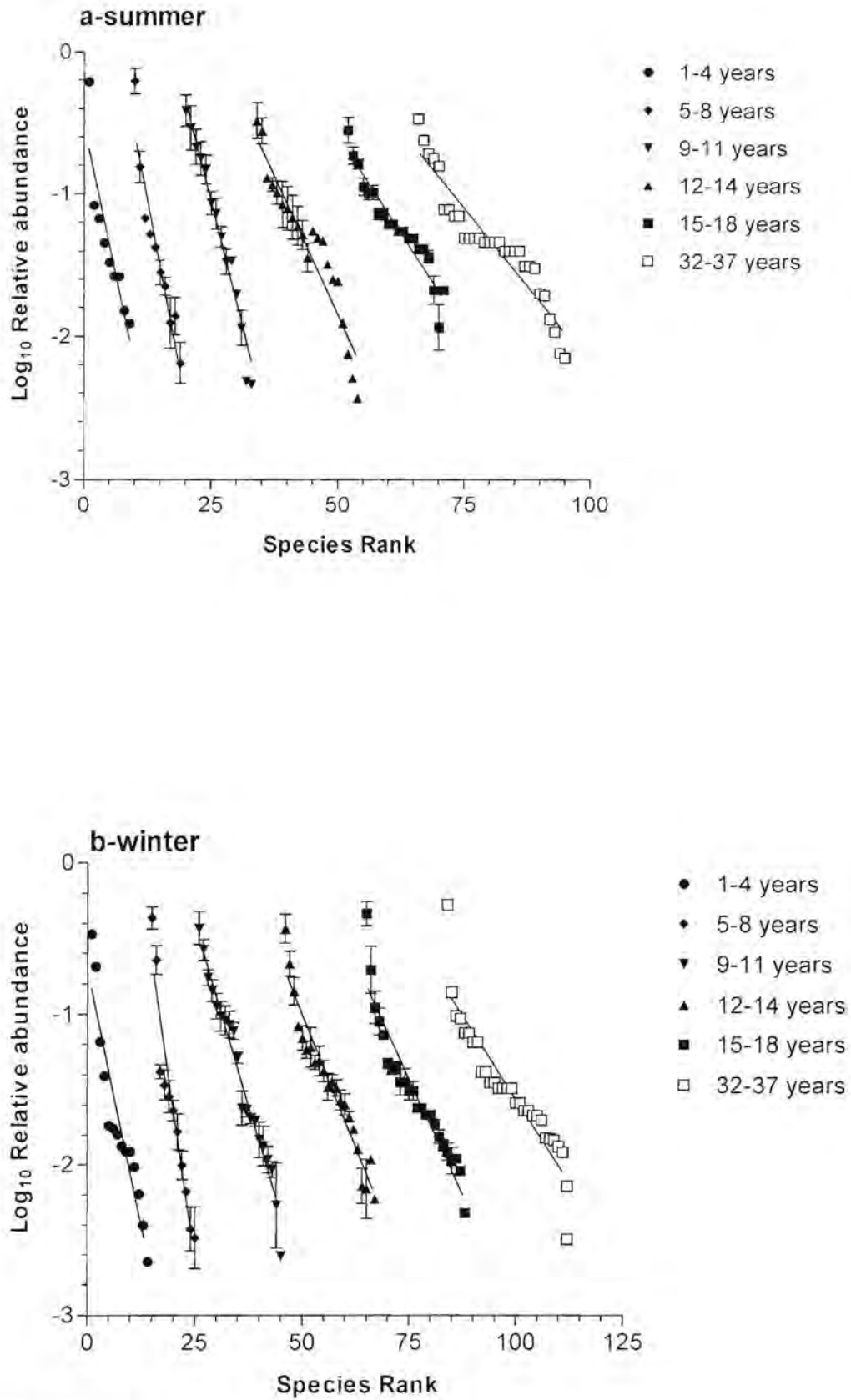


Figure 3: Rarefaction curves based on the relative densities of the bird species during the summers and winters of 1993/94 (a and b) and 1998/99 (c and d) respectively.



(Fig. 4. continue)

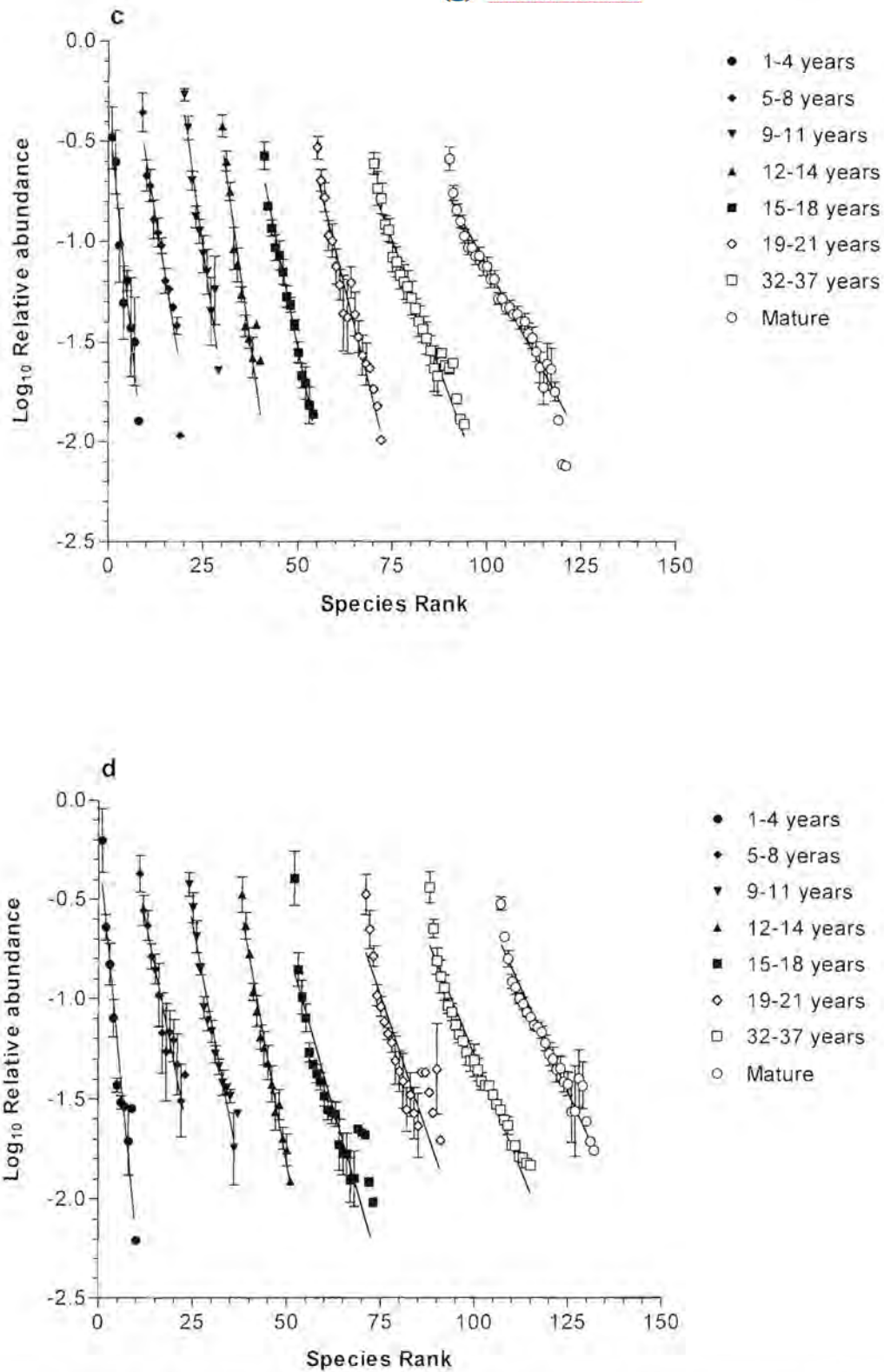


Figure 4: Rank-abundance curves as a function of coastal dune regenerating age based on linear least squares regression analyses of \log_{10} relative abundances and abundance ranks for data collected during the summers and winters of 1993/94 (a and b) and 1998/99 (c and d) respectively.

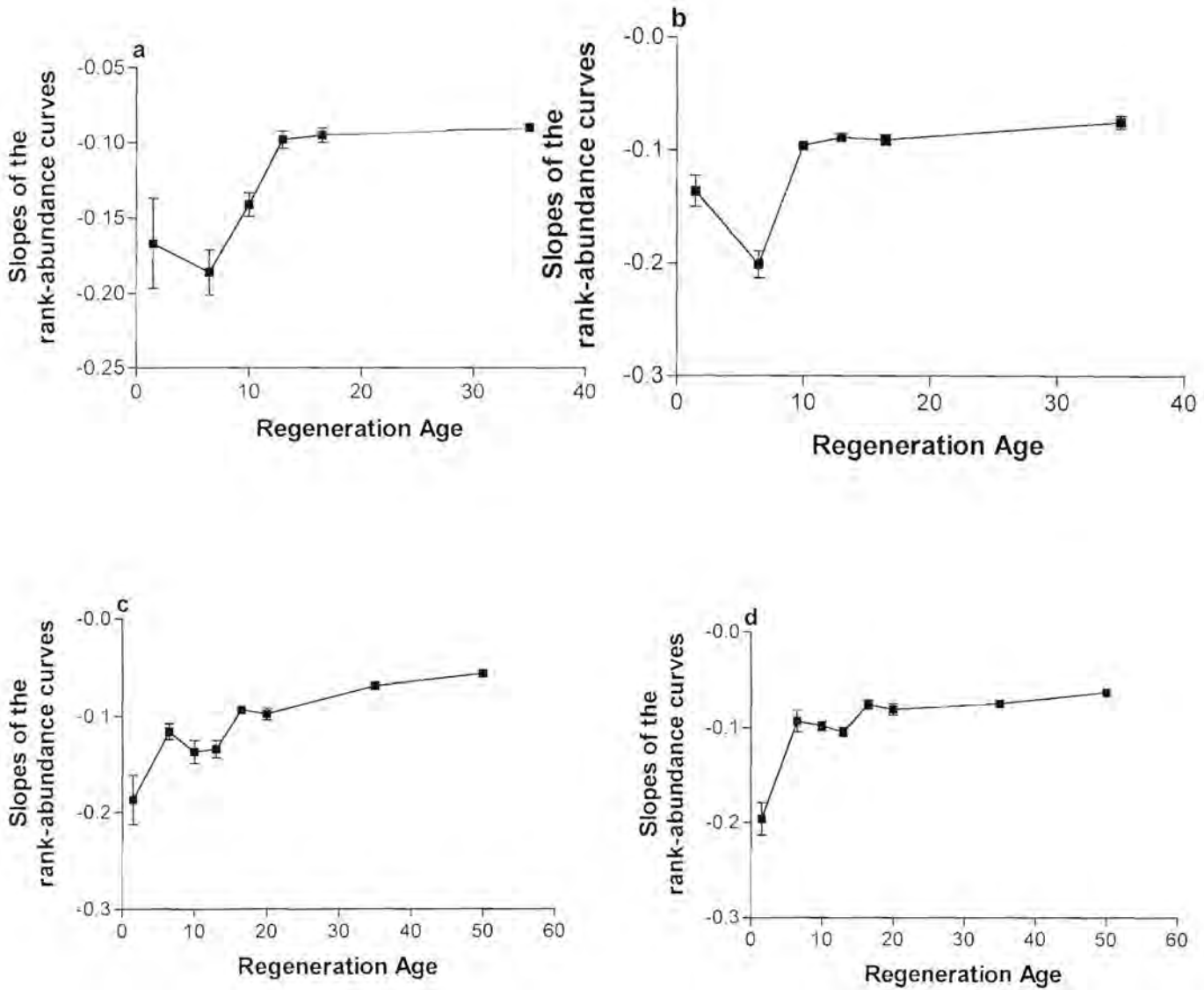


Figure 5: The relative abundance slopes of each sampling site obtained from rank-abundance curves during the summers and winters of sampling periods 1993/94 (a and b) and 1998/99 (c and d) plotted against coastal dune regeneration age.

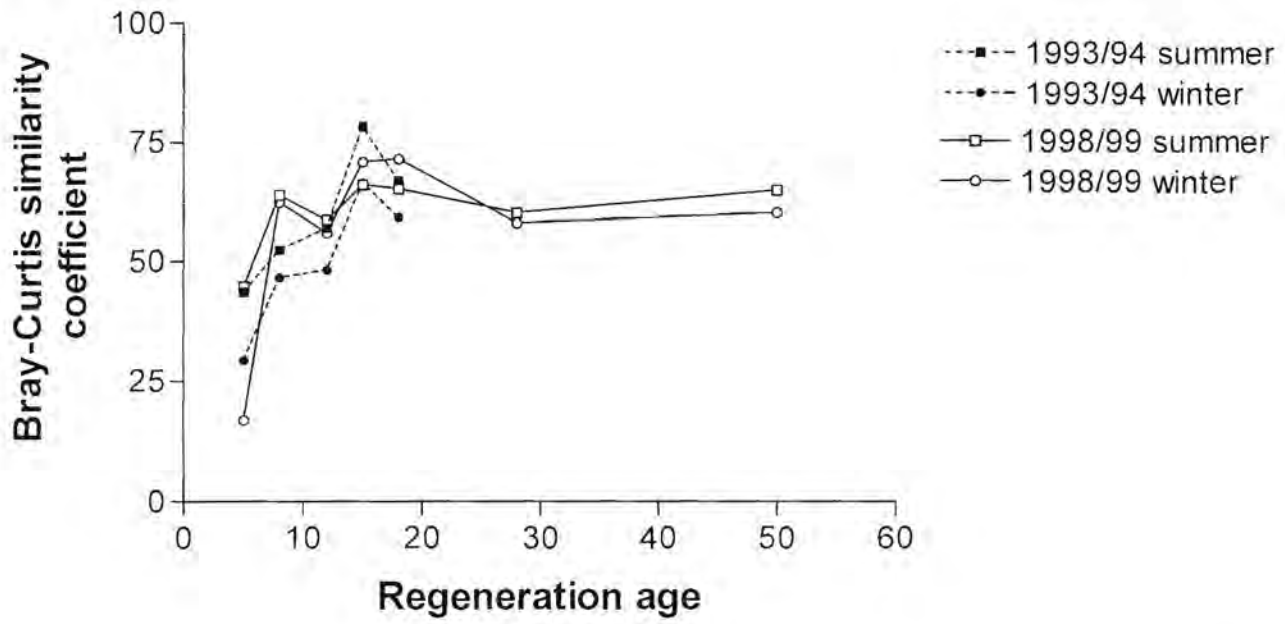


Figure 6: Trends in the Bray-Curtis similarity coefficients of bird communities as a function of regeneration age during two seasons and two sampling years (1993/94 and 1998/99).

three distinct assemblages. The first comprised the 1 to 5 year old sites, the second the 5 to 11 year old sites and the third of sites older than 11 years of age. (Fig. 7a, ANOSIM Global $R=0.83$, $p<0.05$). When data were grouped into seasons, a consistent pattern was recorded for both summer and winter (Fig. 7b, ANOSIM Global $R=0.72$, $p<0.05$; Fig. 7c, ANOSIM Global $R=0.78$, $p<0.05$).

During 1998/99, four assemblages could be distinguished (ANOSIM Global $R=0.80$, $p<0.05$) (Fig. 8a). The first comprised the 1-4 year old site, the second the 5-11 year old sites, the third of sites older than 11 years and the fourth of a small section (one transect) of the unmined mature forest. However, during the winter the 9-11 year old site was more similar to the assemblages >12 years old (ANOSIM Global $R=0.66$, $p<0.05$) (Fig. 8c). The summer assemblage composition was similar (ANOSIM Global $R=0.77$, $p<0.05$) (Fig. 8b) and followed the same trend when data for the seasons were pooled (Fig. 8b).

Typical species

Species typical for each sampling site are presented in Table 10. Here only the species that cumulatively contributed 50% to the mean within-site similarity are presented.

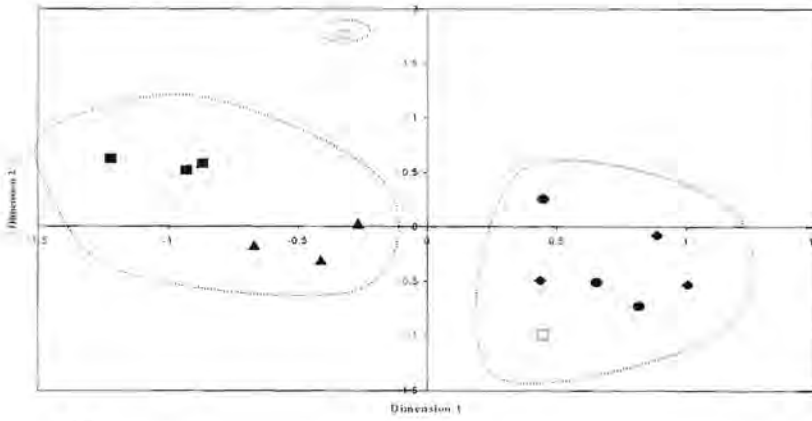
Typical species during summer 1993/94

Species typical for each of the sampling sites less than nine years of age differed from those typical for the 9-14 year old sites. Rattling Cisticola and Yellow Weaver stood out as the typical species during these early stages of forest regeneration, whereas Tawnyflanked Prinia *Prinia subflava*, Bleating Warbler and Yellowbreasted Apalis were typical during later developmental stages (9-14 years). Yellowbellied Bulbul and Forest Weaver *Ploceus bicolor* were typical species on sites >15 years of age.

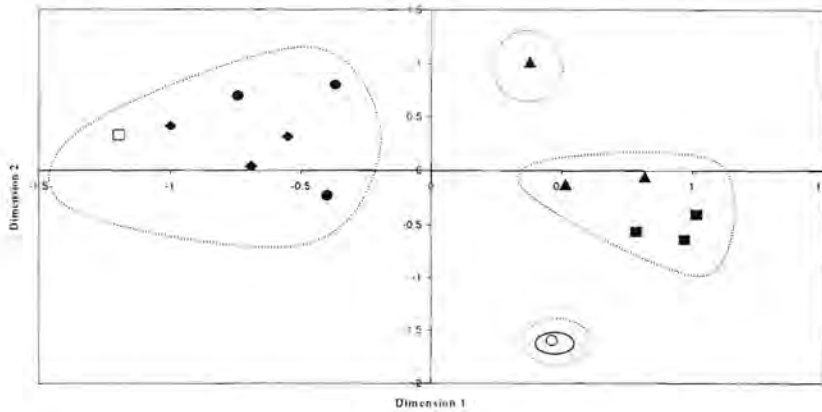
Typical species during winter 1993/94

Rattling Cisticola, Bleating Warbler and Tawnyflanked Prinia were typical species of mid-successional stages (9-14 years). At older developmental stages (12-18 years) Pallid Flycatcher and Yellowbreasted Apalis became more typical, while Yellowbellied Bulbul and Forest Weaver became less typical.

a.



b.



c.

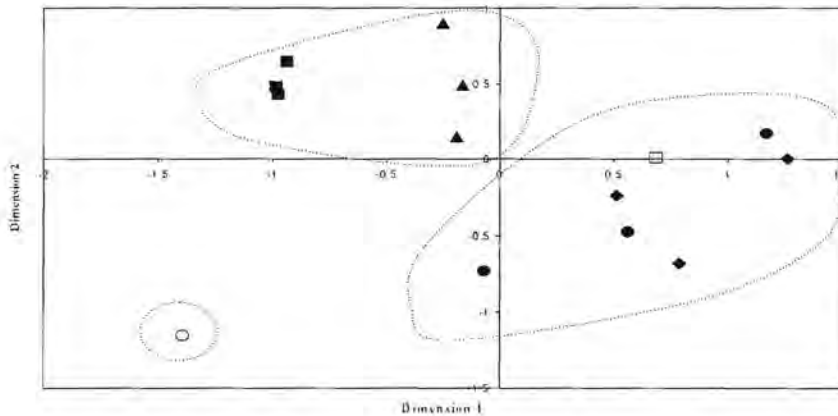


Figure 7: Two dimensional non-metric multidimensional scaling ordination of the relative densities of species based on ranked Bray-Curtis similarities of the bird assemblages of each sampling site during the 1993/94 sampling period. MDS of each site for pooled seasons (stress = 0.07) (a), MDS of each site for summer (stress = 0.07) (b) and MDS of each site for winter (stress = 0.08) (c). (○ denote 1-4 year old site, ■ 5-8 year old site, ▲ 9-11 year old site, ● 12-14 year old site, ◆ 15-18 year old site and □ 32-37 year old site). Each symbol represents the value for a transect.

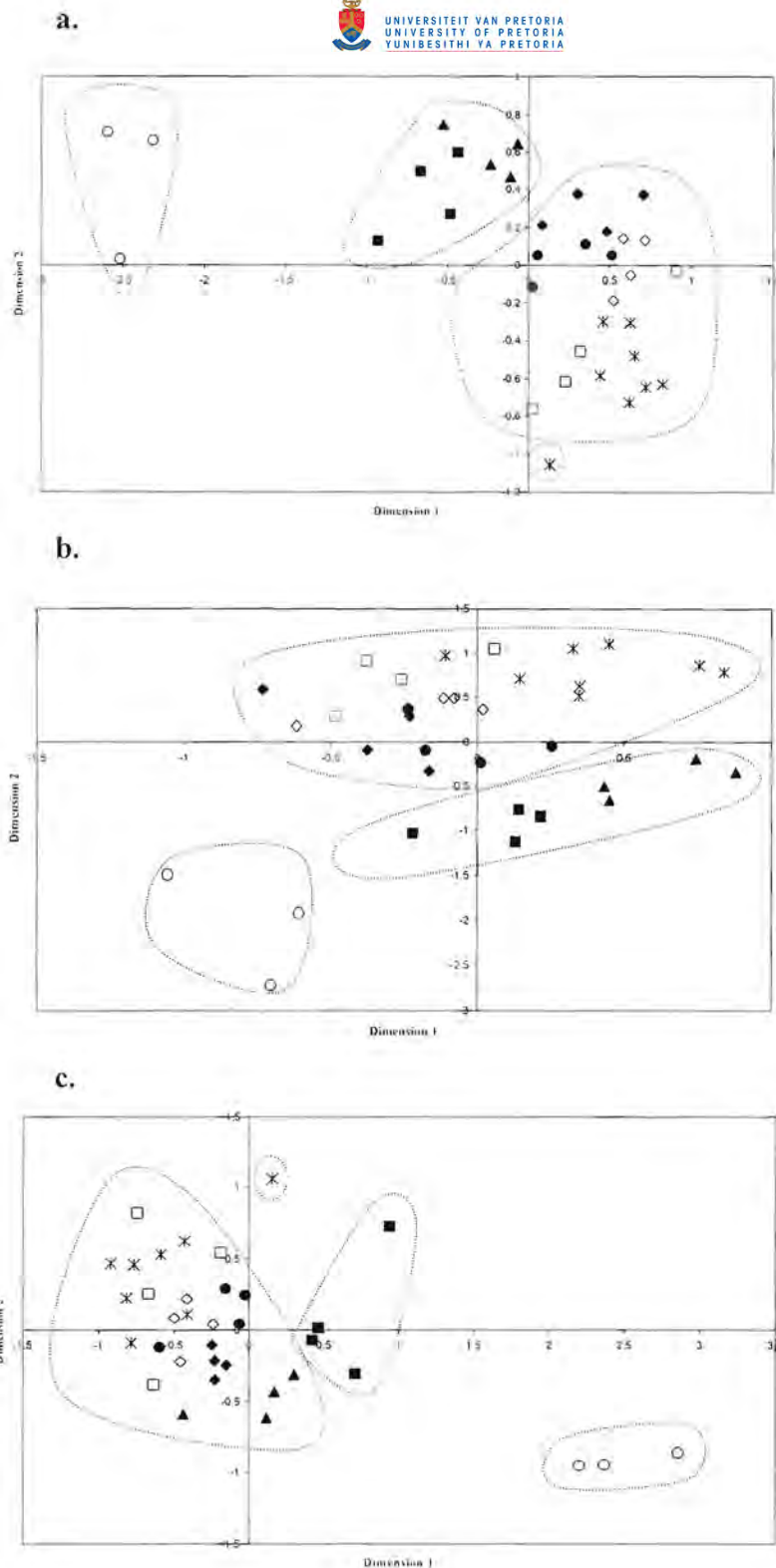


Figure 8: Two dimensional non-metric multidimensional scaling ordination of the relative densities of species based on ranked Bray-Curtis similarities of the bird assemblages of each sampling site during the 1998/99 sampling period. MDS of each site for pooled seasons (stress = 0.12) (a), MDS and dendrogram of each site for summer (stress = 0.14) (b) and MDS of each site for winter (stress = 0.15) (c). (○ denote 1-4 year old site, ■ 5-8 year old site, ▲ 9-11 year old site, ● 12-14 year old site, ◆ 15-18 year old site, ◇ 19-21 years old site, □ 32-37 year old site and * a mature coastal forest. Each symbol represents the value for a transect.

Table 10: Typical species and their percentage contribution to mean within-site similarity for each of the sampled sites during both study periods (1993/94 and 1998/99). Only species contributing cumulatively 50% to the with-in site similarity are listed as typical species.

Sampling site (years)	Summer study period 1993/94			Summer study period 1998/99		
	Species	Consistency	% Contribution	Species	Consistency	% Contribution
1-4	No data	No data	No data	Rattling Cisticola	5.38	36.58
5-8	Rattling Cisticola	12.77	24.43	Bleating Warbler	6.78	18.29
	Yellow Weaver	64.59	13.89	Rattling Cisticola	5.68	17.45
9-11	Tawnyflanked Prinia	34.07	19.93	Bleating Warbler	12.49	23.27
	Bleating Warbler	6.74	19.41	Lesser Masked Weaver	8.56	17.91
12-14	Yellowbreasted Apalis	3.42	22.57	Yellowbreasted Apalis	6.83	22.85
	Bleating Warbler	3.7	17.11	Bleating Warbler	9.09	20.58
15-18	Yellowbreasted Apalis	13.88	15.92	Bleating Warbler	24.4	17.38
	Bleating Warbler	7.87	12.6	Yellowbreasted Apalis	21.3	15.67
	Yellowbellied Bulbul	15.23	10.97	Squaretailed Drongo	12.94	11.32
	Forest Weaver	28.35	10.34			
19-21	No data	No data	No data	Bleating Warbler	7.23	17.05
				Yellowbreasted Apalis	6.93	15.29
				Cape White-eye	6.27	14.77
32-37	No data	No data	No data	Olive Sunbird	8.11	13.79
				Bleating Warbler	3.01	13.14
				Yellowbreasted Apalis	7.89	11.24
				Cape White-eye	7.42	10.5

Mature	No data	No data	No data	Yellowbellied Bulbul	5.16	11.11
				Bleating Warbler	5.43	9.19
				Yellowbreasted Apalis	8.46	9.11
				Natal Robin	7.4	8.48
				Terrestrial Bulbul	1.61	7.44

(Table 10 continue)

Sampling site (years)	Winter study period 1993/94			Winter study period 1998/99		
	Species	Consistency	% Contribution	Species	Consistency	% Contribution
1-4	No data	No data	No data	Common Waxbill	10.81	26.19
5-8	Rattling Cisticola	11.96	21.98	Bleating Warbler	5.94	23.07
	Yellow Weaver	26.22	21	Tawnyflanked Prinia	5.7	20.05
9-11	Rattling Cisticola	5.6	14.2	Bleating Warbler	16.91	18.93
	Bleating Warbler	6.63	11.84	Yellowbreasted Apalis	5.17	17.57
	Tawnyflanked Prinia	42.97	10.47			
	Yellowbreasted Apalis	24.95	10.2			
12-14	Yellowbreasted Apalis	19.49	16.24	Yellowbreasted Apalis	6.37	16.05
	Pallid Flycatcher	56.25	15.71	Bleating Warbler	6.24	14.08
	Bleating Warbler	11.62	13.24	Blackeyed Bulbul	49.28	13.54
15-18	Yellowbreasted Apalis	9.82	18.85	Lesser Masked Weaver	9.18	16.18
	Bleating Warbler	8.7	14.28	Yellowbreasted Apalis	15.3	11.41
	Blackeyed Bulbul	7.98	13.04	Bleating Warbler	4.82	10.25
				Yellow Weaver	6.58	9.51
19-21	No data	No data	No data	Yellowbreasted Apalis	6.97	14.72
				Bleating Warbler	5.63	14.18
				Natal Robin	11.35	11.1
32-37	No data	No data	No data	Sombre Bulbul	4.96	21.18
				Bleating Warbler	12.69	14.37
				Olive Sunbird	4.44	13.18

Mature	No data	No data	No data	Yellowbellied Bulbul	7.6	14.87
				Bleating Warbler	5.28	14.18
				Sombre Bulbul	1.67	10.4
				Olive Sunbird	1.59	9.34

Typical species during summer 1998/99

Rattling Cisticola was typical for the younger sites (1-8 years). During later development (9-21 years) Bleating Warbler and Yellowbreasted Apalis were consistently the most typical species, though a few others contributed erratically towards the typical species lists. The unmined sites were typified by a range of species not recorded on the younger sites (Olive Sunbird, Cape White-eye, Natal Robin and Terrestrial Bulbul *Phyllastrephus terrestris*). These species were almost all recorded with equal consistencies and were therefore equal in status.

Typical species for during 1998/99

Common Waxbill represented the typical species on young sites. Bleating Warbler, Yellowbreasted Apalis and Blackeyed Bulbul *Pycnonotus barbatus* were typical of older sites (9-14 years). As forest development progressed (from 15 years onwards) Natal Robin became typical, followed by Bleating Warbler and Yellowbellied Bulbul on the unmined mature site. Typical species therefore differed between study periods as well as between sampling occasions within a study year.

Discriminant species

Species replacements, as implied by between-sampling site differences in discriminant species, are presented in Table 11.

Discriminant species during summer 1993/94

Fantailed Cisticola consistently occurred on the early developmental (1-4 years) sites together with more erratic species, such as Grassveld Pipit *Anthus cinnamomeus* and Yelloweyed Canary *Serinus mozambicus*. On 5-8 and 9-11 year old sites Bleating Warbler, Puffback *Dryoscopus cubla* and Tawnyflanked Prinia appeared as discriminant species. Sites >12 years of age were characterised by Puffback as a discriminant species. Species such as Redeyed Dove *Streptopelia semitorquata*, Grey Waxbill *Estrilda perreini* and Yelloweyed Canary discriminated the 32-37 year old site from other age classes.

Table 11: Discriminant species contributing cumulatively to 50% of the between-site dissimilarity of sites of known age sampled during 1993/94 and 1998/99. *** = best discriminant species, ** = second best discriminant species and * = the third best discriminant species. Weavers[†] refers to mixed flocks of Yellow and Lesser Masked Weavers. Golden R.T. Barbet[‡] refers to Goldenrumped Tinker Barbet.

Discriminating sites	Species	Consistency	% Contribution
Summer 1993/94			
1-4 years	Grassveld Pipit	28.89	10.88
5-8 years	Fantailed Cisticola	33.85*	9.89
	Yelloweyed Canary	28.89	9.15
5-8 years	Bleating Warbler	6.3**	11.07
9-11 years	Fantailed Cisticola	8.87***	8.09
	Rattling Cisticola	1.82*	6.54
9-11 years	Tawnyflanked Prinia	5.09**	8.97
12-14 years	Rattling Cisticola	1.91*	7.36
	Puffback	9.1***	5.53
12-14 years	Forest Weaver	1.49*	7.55
15-18 years	Weavers [†]	1.52**	6.86
15-18 years	Redeyed Dove	33.53	8.44
32-37 years	Grey Waxbill	33.53	7.09
	Yelloweyed Canary	33.53	7.09
Summer 1998/99			
1-4 years	Bleating Warbler	4.46**	12.09
5-8 years	Yellowbreasted Apalis	3.49*	9.63
	Whitebrowed Robin	6.56***	9.09
5-8 years	Rattling Cisticola	6.2***	13.83
9-11 years	Lesser Masked Weaver	2.04**	10.73
	Forest Weaver	1.58*	9.01
9-11 years	Cape White-eye	4.32***	10.27
12-14 years	Lesser Masked Weaver	2.51**	10.27
	Rudd's Apalis	1.66*	7.64
12-14 years	Blackeyed Bulbul	1.17***	5.99
15-18 years	Olive Sunbird	1.14**	5.42
	Squairetailed Drongo	1.13*	5.02
15-18 years	Natal Robin	1.59***	6.63
19-21 years	Puffback	1.17**	4.72
	Blackeyed Bulbul	1.15*	4.49
19-21 years	Golden R.T. Barbet [‡]	1.59***	5.86
32-35 years	Tawnyflanked Prinia	1.56**	5.19
	Olive Sunbird	1.53*	4.6
32-35 years	Terrestrial Bulbul	1.71***	4.75
Mature	Cape White-eye	1.63**	4.57
	Tawnyflanked Prinia	1.43*	3.67

(Table 11 continue)

Winter 1993/94			
1-4 years	Bronze Mannikin	16.53	10.7
5-8 years	Grassveld Pipit	16.53	6.84
	Common Waxbill	16.53	6.73
5-8 years	Yellow Weaver	2.15*	9.59
9-11 years	Blackeyed Bulbul	2.22**	5.05
	Rattling Cisticola	2.66***	4.91
9-11 years	Rattling Cisticola	6.07**	7.12
12-14 years	Pallid Flycatcher	5.52*	6.8
	Dusky Flycatcher	13.06***	4.65
12-14 years	Pallid Flycatcher	1.46**	4.4
15-18 years	Cape White-eye	1.29*	3.8
	Burchell's Coucal	1.74***	3.71
15-18 years	Redeyed Dove	10.72	6.61
32-37 years	Tawnyflanked Prinia	10.72	4.89
	African Goshawk	10.72	4.42
Winter 1998/99			
1-4 years	Common Waxbill	7.38**	10.7
5-8 years	Bleating warbler	4.47*	8.11
	Stonechat	8.62***	6.5
5-8 years	Rattling Cisticola	1.59*	6.46
9-11 years	Yellowbellied Bulbul	7.43***	6.26
	Forest Weaver	1.65**	4.88
9-11 years	Sombre Bulbul	2.13***	7.02
12-14 years	Rudd's Apalis	1.65*	5.67
	Squaretailed Drongo	1.67**	4.62
12-14 years	Lesser Masked Weaver	3.07**	11.28
15-18 years	Whitebrowed Robin	10.01***	6.37
	Black Cuckooshrike	1.66*	5
15-18 years	Yellow Weaver	6.23***	8.73
19-21 years	Lesser Masked Weaver	1.72**	8.34
	Collared Sunbird	1.71*	7.05
19-21 years	Yellowbreasted Apalis	1.81**	6.81
32-35 years	Olive Sunbird	1.84***	5.03
	Sombre Bulbul	1.57*	4.4
32-35 years	Yellow Weaver	1.41***	3.82
Mature	Puffback	1.16*	3.54
	Southern Boubou	1.23**	3.43

Discriminant species during winter 1993/94

Common Waxbill, Bronze Mannikin and Grassveld Pipit represented discriminant species on the 1–4 year old site, while Rattling Cisticola and Yellow Weaver became less numerous and Blackeyed Bulbul and Dusky Flycatcher *Muscicapa udusta* appeared as discriminant species on the 5 to 11 year old sites. Further development (sites >12 years old) saw the appearance of Burchell's Coucal *Centropus burchellii*, Redeyed Dove, and African Goshawk *Accipiter tachiro* as discriminant species.

Discriminant species during summer 1998/99

The 1-4 year old site contained no woodland bird species, typical of those found at stages of later development (5-11 years), e.g. Whitebrowed Robin *Erythropygia leucophrys* and Bleating Warbler. As forest development continued (12 years and onwards), Cape White-eye appeared while Lesser Masked Weaver and Rudd's Apalis *Apalis ruddi* were absent. Blackeyed Bulbul, Natal Robin, and finally Goldenrumped Tinker Barbet *Pogoniulus bilineatus*, appeared as discriminant species. Terrestrial Bulbul only occurred in high numbers on relatively mature forests >32 years of age.

Discriminant species during winter 1998/99

The replacement of species during the winter differed from that described for summer. The sites representing early stages of development (1-4 years) harboured Stonechat *Saxicola torquata* and Common Waxbill as discriminant species. Yellowbellied Bulbul, Forest Weaver and Rudd's Apalis appeared during later development (5-11 years) while Yellowbellied Bulbul disappeared. During later development (12 years and onwards) these latter species were recorded less frequently, while Sombre Bulbul and Squaretailed Drongo *Dicrurus ludwigii* appeared as discriminant species. Olive Sunbird, Yellow Weaver and Southern Boubou *Laniarius ferrugineus* emerged as discriminant species on forests >32 years of age. Discriminant species, like typical species, differed between study periods as well as between sampling sites within a study year.

Discussion

Community structure and development

Along a successional gradient, the rate of species replacement is expected to decrease from early to late development, where as species additions are expected to increase (Myser & Pickett 1994). In the present study, the development of coastal dune vegetation in response to post-mining rehabilitation was associated with an increase in the number of bird species with an increase in regeneration age. Early stages (1-4 years old) of regenerating coastal dune forest were dominated by pioneer species with Rattling Cisticola, Common Waxbill, Fantailed Cisticola and Bronze Mannikin (Fig. 2) persisting at relatively high densities. Sites representing later seral stages (5-11 years old) of vegetation regeneration were dominated by secondary species (Bleating Warbler and Yellowbreasted Apalis) with specialists (Terrestrial-, Sombre- and Yellowbellied Bulbul, Olive Sunbird and Natal Robin) occurring at low numbers while pioneer species no longer occurred.

The early development of the bird community was therefore characterized by an increase in the number of species through the addition as well as replacement of species. These changes were associated with a decrease in the relative contribution of each species to the community. The increase in the number of bird species with an increase in habitat regeneration age is typical of succession (see May 1982, Van Aarde *et al.* 1996a, Van Aarde *et al.* 1996b, Kritzing & van Aarde 1998). In such cases early development is characterised by a few species occurring at relatively high densities. Later development is characterised by the presence of relatively more species, though these occur at relatively lower numbers (see Table 4). A similar trend has also been recorded for other taxa occurring in the study area (Major & De Kock 1992, Lubke *et al.* 1992, Vogt 1993, Ferraira 1995, Ferreira & van Aarde 1997) as well as over a range of different habitats (Shugart & James 1973, Smith & MacMahon, 1981, James & Wamer 1982, May 1982). Therefore, more species were added, with fewer species replacements, to assemblages on older regenerating coastal dune vegetation and mature forests than assemblages on younger regenerating vegetation.

In the present study, the increase of absolute density with an increase in regeneration age during both study years did not follow a monotonic trend. Density is expected to increase with regeneration age only if the ability of the habitat to sustain individuals also increases with regeneration age. In keeping with the findings of other studies (e.g. Kendeigh 1946, Karr 1968, Shugart & James 1973, Probst *et al.* 1992,

Westworth & Telfer 1993), intermediate successional stages housed lower densities than early and late successional stages or mature forests. During early successional stages pioneer species are known to increase rapidly in density in response to disturbance events (Ferreira 1993) and are one of the main reasons for this bimodality observed in density. For species to show a monotonic trend only a few species should be dominant throughout the study area, or the species pool should be constrained to limited resources (Bowers & Harris 1994). During later successional stages as well as in mature forests, increased density should be associated with an increase in the range of habitats occupied by a species, as increased competition forces some individuals to occupy marginal habitats (Wiens 1989). Values for bird densities were also far greater during the first study period (1993/94) than in same-age sites during the second study period.

Species diversity increased with habitat age (for both study periods), with values converging to those recorded for the unmined forests. In spite of this, diversity on the oldest regenerating site was still lower than that of the relatively mature forests (see Table 4). When considering the age of the regenerating sites (1-21 years at the time of the study), this relatively low diversity in even the oldest regenerating sites may occur as they still only represent relatively early to mid-successional stages of forest development and not a complete successional sere. The relatively young age of these regenerating sites, in comparison to the unmined forest, may also explain the bimodal density pattern.

Rarefaction curves for the present study confirm the observed pattern of increasing bird species diversity with increasing habitat age. Thus, the recorded increase in diversity in the present study represents a true increase and not a sampling artefact. The rank-abundance curves illustrate that numerical dominance decreased and equitability increased with habitat regeneration age. This increased equitability was further confirmed by the reduction in the steepness in the slopes of rank-abundance curves with increased regeneration ages (Figures 4 & 5).

Many processes and various models have been proposed to explain the above-mentioned trends in diversity. The geometric (Whittaker 1965) and broken stick (MacArthur 1957) models are such resource-apportioning models, based on the underlying ecological theory (Bastow 1991). Based on these models, the most competitive and successful early successional pioneer species (for which assemblages are described by steep rank-abundance slopes), will take a relatively large fraction of

the resources, while the second most successful species will take a fraction of the remaining portion. During later successional stages (when the slopes of the rank-abundance curves are shallower), the greater number of species within the community promotes a more random partitioning of these resources along a one-dimensional gradient, and will displace any early pioneer species (Wiens 1989). However, Ricklefs (1987) showed that local diversity depends on regional diversity. Thus, it is likely that species diversity in relatively small areas such as those of the regenerating sites, may be dependent on the availability of similar habitat at a regional scale (Karr 1976).

Kritzinger & van Aarde (1998) postulated that undisturbed habitats dominated the region before the advent of modern anthropogenic activities, therefore predicting that the bird community of the region would be dominated by species adapted to historically undisturbed habitats. Thus, undisturbed areas should have a higher diversity than rehabilitating areas, and with increasing age and regeneration the rehabilitating areas should become more similar to undisturbed forests. This results from species typical of undisturbed areas colonising regenerating areas. My results showed that undisturbed areas (such as mature forests) have a higher diversity than the rest of the study area (see Figures 3 & 4) and that older regenerating areas harboured more species than younger sites (see Figures 3 & 4), thus confirming the prediction of Kritzinger & van Aarde (1998).

Additionally, several authors have explained differences in diversity among habitats by differences in foliage height diversity (MacArthur 1964, MacArthur & MacArthur 1961, MacArthur *et al.* 1966, Wilson 1974, James & Wamer 1982). Removal of foliage height diversity through mining, followed by its rehabilitation during habitat regeneration, may also contribute to the increase in bird diversity with habitat regeneration age.

Community composition

Along a successional gradient a collection of individuals of several species that co-occur can be identified as a discrete community (Wiens 1989). Such communities can be identified by a specific set of species within its geographical border and each community would therefore have a distinct species composition (Begon *et al.* 1990). These communities are expected to transform along a successional gradient through a series of species losses and additions. With succession, associated trends in the

biology of their reproductive rates and patterns, and their ecological niches are also expected to change through time (May 1984, Mönkkönen & Helle 1987, Wiens 1989, McCook 1994, Pacala & Rees 1998). In the present study species that are opportunistic generalists (high reproductive output, widespread and generalised foraging strategies, e.g. cisticolas and waxbills) were replaced by more specialised species (low reproductive output, localised ranges, specialised foraging strategies e.g. hornbills and barbets) typical of undisturbed forests. Similar findings have been made for the successional avifauna elsewhere (Odum 1969, Pickett 1976, May 1982, Mönkkönen & Helle 1987, Bowers & Harris 1994).

Multidimensional scaling suggests that three discrete bird assemblages could be identified, these representing early, intermediate and late successional assemblages, where the latter comprised regenerating sites older than 12 years of age and those of unmined areas. Importantly, the assemblages on the older rehabilitating sites (sites 12 years and older) could be incorporated with the relatively mature and unmined forest assemblages. Therefore, the bird assemblages on older regenerating stages tend to become more similar in assemblage structure to the unmined forest assemblages.

The development of bird communities of these coastal dune forests may be described by the identification of typical species for each of the sites, as obtained from the MDS analyses. Typical species are those that contribute most consistently to the highest percentage of relative densities within the sampled sites. Therefore, the typical species will invariably be the most abundant species within their respective habitats. This does not mean, however, that those species with the highest percentage contribution to relative density will be considered as typical. A species that contributes more consistently to relative densities will be a more typical species than one with higher percentage contribution to relative density but with less consistency (Clarke & Warwick 1994).

Species typical of the 1 to 4 year old regenerating dune vegetation, such as Rattling Cisticola and Common Waxbill, persist on suitable habitat in almost any biome throughout their distribution range. As opportunistic generalists (Maclean 1993) they are apparently able to thrive on coastal dune grasslands, typical of sites that have been regenerating for less than four years.

Species typical of the 5 to 11 year old *Acacia* shrublands may favour ecotones (e.g. Cisticolas and Prinias) while others (e.g. Bleating Warbler, Yellowbreasted

Apalis) prefer the dense wooded nature of the area. These species are either insectivores (small leaf-gleaners) (Berruti 1997, Berruti & Allan 1997), or facultative insectivores (e.g. Yellow and Lesser Masked Weavers). However, these species do not necessarily use the area as a breeding site and some prefer to breed outside wooded areas in drainage lines (Maclean 1993, Craig 1997). In the present study species composition on the early- to mid- successional stages mostly represents generalist species that occupy a variety of habitats within their geographical distribution range. These species clearly are able to colonise coastal dune habitats that have been regenerating for less than 11 years.

Several authors have predicted that later development stages of forest regeneration may be typified by bird species with traits such as relatively low fecundity, limited dispersal abilities, slow growth and an ability to co-exist in a species rich environment (Connel & Slayter 1977, Tilman 1988, Pacala & Rees 1998). In the present study, such species are all insectivores, either as leaf-gleaners or probers (e.g. Forest Weaver, Berruti & Allan 1997, Day 1997, Craig 1997), or omnivores (e.g. Blackeyed Bulbul, Hart 1997). These species occurring in later development stages of forest regeneration are relatively large (21.1-52.9 grams, Maclean 1993), breed seasonally and have small clutches (2-3 eggs, Maclean 1993). Species typical of early stages of development are relatively small (ranging from a mean of 8.2 grams in the smallest species to 17.5 grams in the larger species) and produce clutches containing 4-6 eggs (Maclean 1993, Harrison 1997). Such species are typical colonists of woodlands, although I recorded Bleating Warbler and Yellowbreasted Apalis in reasonable numbers on pristine and unmined coastal dune forests.

Resource specialists such as nectar- and fruit-eating species typified the unmined study sites representing late stages of dune forest development. Sunbirds and various species of fruit-eating bulbuls (Sombre, Yellowbellied) frequent these areas where nectar rich plants (e.g. *Strelitzia nicolai* (Regel & Koern)) and fruit bearing trees (e.g. *Allophylus natalensis* (De Winter)) are common. These sites are also characterised by a marked increase in undergrowth, where habitat specialists such as Natal Robin occur (Kritzinger 1996, Oatley 1997). Most of these species have traits different to those of species typical of the early developmental stages, such as high site fidelity through specialised habitat and resource preference (Oatley 1997, Tree 1997).

Although typical species for the two study years for a specific stage of community development differed (see Table 10) birds associated with the post-mining regeneration of coastal dune vegetation follows MacArthur's $r - K$ -selection continuum (MacArthur & Wilson 1967). Species typical of early successional stages appear to be r -selected (generalists with high dispersal rates, small sizes and large clutches e.g. Rattling Cisticola and Common Waxbill) while typical species of late successional species appear K -selected (specialist with high site fidelity e.g. Natal Robin and Terrestrial Bulbul).

Species dominating the 1 to 4 year old sites (Cisticolas, Bronze Mannikin, Common Waxbill) are of similar size and feed primarily on grass seeds (Barnard 1997, Nuttall 1997). Other species living here, such as Pipits, Stonechats, and Yelloweyed Canary also utilise grass seeds and prefer open habitats to wooded areas (Clancey 1997, Harrison 1997, Nuttall 1997).

The intermediate stages of regeneration (5-11 years) were occupied by species (Tawnyflanked Prinia, Blackeyed Bulbul, Bleating Warbler, Whitebrowed Robin, Rudd's Apalis and Cape White-eye) that were also present on the older developmental stages. They appear to occur more consistently in more open woodlands than in the more closed habitat offered by true dune forests (see Table 11). All these species are common and widespread within their distributional ranges, except for Rudd's Apalis, which is a Maputaland endemic (Maclean 1993, Day 1997).

The bird assemblages on the later stages of development were dominated by late successional species such as Sombre Bulbul (winter), Squaretailed Drongo, Blackeyed Bulbul (summer), Olive Sunbird and Natal Robin. These birds inhabit an area comprising relatively tall stands of *Acacia* trees (Terborgh & Robinson 1986) with a relatively dense undergrowth habitat (Van Aarde *et al.* 1996b). This assemblage is dominated by habitat specialists, which were only recorded on unmined sites. However, the majority of these species do not occur at numbers high enough to be identified as discriminant species. Some are hole-nesters (barbets, hornbills), utilising a resource that would not be available in the younger, regenerating stands. Others attain relatively high body mass, including non-passerines such as Redeyed Dove (mean body mass 252g) and raptors such as African Goshawk (mean body mass 342g; Maclean 1993). Most raptors species recorded during the study occurred in the later stages of dune forest development and especially the unmined sites. The unmined areas also support the highest numbers of nectar feeders (4 species of

sunbirds) and fruit-eaters (4 species of bulbuls). It would appear that large dead trees might be needed for the survival of many non-passerines, especially cavity nesters (Kritzing 1996).

The diverse composition of these assemblages may be due to the unmined forest itself comprising a collection of regenerating stages representative of a coastal dune forest sere. This mosaic of developmental stages can be ascribed to small-scale disturbance events creating gaps that initiate small-scale successional development. Schemske & Brokaw (1981) and Levey (1988) also found that such gaps in forests produce more fruit- and nectar bearing plants, which attract frugivores and nectarivores. Therefore, it is not unlikely that gaps caused by treefalls would affect the distribution of frugivores and fruit bearing plants in this area.

Besides the differences in species life-history traits along the successional sere in my study area, there were also differences in the typical and discriminant species recorded between the two study periods. Although some of the species differ between the two study periods they share the same life-history traits (e.g. all insectivores and share the same body mass and reproductive output), while the only differences between species were the way they exploited the available resources. This, together with the fact that different species were recorded at different times of the year (seasonal differences), implies that some structural change should have taken place in their habitat. Also, more species were recorded during 1993/94 than 1998/99 and at higher densities during summer than winter. Structural changes to habitat due to climatic fluctuations (temperature changes) are known to have a marked effect on resource availability and increased visibility in winter increases predation and would explain the decrease in species numbers during winter (Samways 1994). Increased visibility in winter is also influenced by the increased activity of birds when food resources become scarce, or the possibility of lower foliage density making the birds more conspicuous during the sampling process. Besides these factors, inter-seasonal differences appeared to be minimal during 1998/99 and species numbers were markedly lower. I can only assume that increased regeneration between sampling years might suggest stability upon succession and lower the observed variability recorded during earlier sampling.

Therefore, changes in bird community structure on the regenerating dunes of Richards Bay appear to support some theoretical models of succession, and are very similar to other studies on forest succession.

Habitat-regeneration-age related trends in the characteristics of the bird assemblages were similar in community structure and, to a lesser extent, their species compositions over the two study periods. Bird species specialisation increased with habitat age during both study periods and seasons, thus supporting the assumption of Kritzinger & van Aarde (1998). The colonisation of regenerating sites, through species additions and replacements, probably results from habitat requirements being fulfilled through the development of vegetation heterogeneity (Van Aarde *et al.* 1996). Furthermore, the species compositions on the different stages of development differed considerably from each other as well as for different time periods (seasons) within a sere and it therefore appears that ecological succession is driving the development of the communities from relative simple (early stages with few pioneers) to relatively complex (later development stages with several more specialist) communities.

Chapter 4

Disturbance and coastal dune bird assemblages at local and regional scales in northern KwaZulu-Natal, South Africa

Introduction

Several authors have suggested that the highest diversity is maintained at intermediate levels of disturbance (Horn 1975, Miller 1982, Petraitis *et al.* 1989). They maintain that increased diversity, in response to intermediate levels of disturbance, may be explained by trade-offs in species-specific abilities constraining immigration and extinction in previously disturbed patches. Therefore, members of the community may either resist disturbance or competition, but not both. Without this trade-off the intermediate disturbance hypothesis can not be maintained. Most studies supporting the intermediate disturbance hypothesis have been conducted on intertidal or planktonic fauna and flora (Sousa 1979, Paine & Levin 1981), whereas many studies on terrestrial animals do not support its predictions (Fuentes & Jaksic 1988). Based on a recent review by Mackey & Currie (2000) very little support exists for the intermediate disturbance hypothesis as a mechanism to explain the observed trends in diversity measures in terrestrial taxa. The existence of a gradient of disturbances of coastal dune forests in KwaZulu-Natal, South Africa serves as a template for the present investigation into the response of bird assemblages to different levels of habitat disturbances.

On the landscape scale the patches of indigenous forests, regenerating dune vegetation of known age and poorly maintained plantations of exotic species in the study area are presenting increasing levels of habitat disturbance. Here sites of post-mining regenerating indigenous coastal dune vegetation may be considered as representing an area of intermediate disturbance, while exotic plantations may be considered as presenting an area of severe disturbance. Patches of relatively undisturbed indigenous forests can be considered as representing undisturbed habitats. Within the regenerating sites there is also a sliding scale of disturbance. Those patches with little time to regenerate may be considered as representing a severe level of disturbance, while those with intermediate recover periods may be considered as

representing an intermediate level of disturbance. Regenerating sites with the maximum recovery period represent the least disturbed level. The scenario presented here thus provides habitat disturbance gradients on both the regional and local scales.

This belt of coastal dune forest falls within the Maputaland-Pondoland regional mosaic of southern Africa (White 1983). The mosaic is the focus of rich floristic endemism (see Van Wyk 1994, 1996) and well known for its high diversity of birds, especially within the coastal dune forests (Harrison *et al.* 1997). Some of the species found here are either endemic to the region, or considered rare due to their low abundances and restricted ranges. As a consequence they may be vulnerable to habitat disturbances (Usher 1986, Simberloff 1988).

The coastal dune forests, regenerating forests and exotic plantations all harbour a variety of indigenous birds. Colonisation of these patches by species atypical of the region could increase species richness through the process of species addition (Schluter & Ricklefs 1993). Alternatively, interspecific interactions may result in a reduction of regional species richness (Schluter & Ricklefs 1993). Thus, the relatively high incidences of disruption and fragmentation may have negative consequences for diversity by effecting species with restricted geographic ranges that occur at low abundances (Cole & Landras 1996, MacNally 1997). The presence of atypical species may also impact on resource availability for species indigenous to the region, while habitat disturbances may create edge effects to the benefit of alien species (Turner 1996, Turner & Corlett 1996). On the other hand, bird species with special conservation status, due to their low abundances or localised ranges may respond positively to habitat alterations resulting from the successional development induced by post-mining dune rehabilitation (Karr 1976, Cody 1981, Kritzinger 1996, Kritzinger & van Aarde 1998).

Based on the intermediate disturbance hypothesis I predict that bird assemblages on regenerating coastal dune vegetation should be more species rich and diverse than those of exotic vegetation and undisturbed coastal dune forests. I also predict that bird assemblages on regenerating vegetation of intermediate age within the regenerating vegetation should be more diverse than those on older and more recent patches within this site. Alternatively, should these predictions not hold, I expect an increase in both species richness and diversity with an increase in habitat heterogeneity. If so, diversity indices for the patches dominated by exotic understoreys and canopies should be lower than those of regenerating indigenous vegetation, while measures for the latter should be less than those for indigenous forests with a diverse

understorey and canopy. In this chapter I also identify rare species for each of the habitat types in order to assess the influence of a gradient of habitat disturbance and regeneration on species populations and assemblages.

Material and Methods

Sampling sites

Three areas were identified as study sites, these representing a gradient of disturbance levels. These are:

- (1) A relatively undisturbed area with Mapelane (28°29'S 32°25'E) and Zulti/Sokhulu (28°30'S 32°25'E), where both the understorey and canopy of these mature dune forests are dominated by a variety of indigenous vegetation. The vegetation of these sites has been described by Venter (1976) and Weisser (1980) (see also Table 2).
- (2) An area of intermediate disturbance comprising six sites where the vegetation is regenerating in response to a post-mining dune rehabilitation programme (see Van Aarde *et al.* 1996a). These represent known-age sites of an indigenous coastal dune successional sere. At the time of the study the ages of these seral stages ranged from a few months old to 21 years, with vegetation diversity indices increasing with regeneration age (see Van Aarde *et al.* 1996a). Here the canopy is dominated by *Acacia karroo* (Hayne). With increasing habitat regeneration age over 20 years this species is replaced by species typical of the mature dune forests of the region (Van Dyk 1997). Other sites representing an intermediate area of disturbance were subjected to disturbances other than mining. Based on tree stem diameters, as an indication of the age of regeneration, these appear to be of similar regeneration age to the 5-8, 9-11 and 19-21 year old regenerating mined sites, while grassland site at Cape Vidal (28°11'S 32°33'E) was maintained through regular burning. Sites regenerating for more than eight years consist of a species rich, indigenous understorey and a homogenous canopy of *Acacia karroo*, while sites less than eight years of age represent grass- and shrubland habitats (see also Table 1 and 2).
- (3) A severely disturbed area comprising sites where both the understorey and canopy are dominated by exotic plant species. These sites are no longer maintained as plantations and as a consequence a dense undergrowth of creepers (e.g. *Achyranthes aspersa* (L.)) and highly invasive shrubs (including *Lantana camara* (L.), *Psidium guajava* (L.) and

Chromolaena odorata (L.) flourish. The canopies are usually dominated by exotic trees such as *Pinus elliotii* (L.), *Eucalyptus grandis* (L'Her) and *Casuarina equisetifolia* (J.R. & G.Forster) (see also Table 2).

Within the area of intermediate disturbance (regenerating sites), three site sub-categories were recognised. All regenerating vegetation sites >14 years were considered to be the least disturbed, sites 5-15 years as intermediate levels of disturbance and sites < 5 years to be severely disturbed.

Data collection and analyses

A full description of the methods to determine density for each transect line and relative density for each species is presented in Chapter 2. Data for the post-mined regenerating sites were obtained from the summer 1998/99 study year database (1 December to 22 December).

Mean species richness (S), Shannon diversity index (H' , \log_e), Pielou's evenness index (E) and the total density (density for all species ha^{-1}) were calculated for each sample site. Differences in mean values were assessed using Kruskal-Wallis One-Way Analyses of ranks and Dunn's distribution free multiple range test (Sokal & Rohlf 1995). Rank-abundance curves were constructed as described by Tokeshi (1993). Least-squares regression analyses were used to fit curves and to compare the slopes generated for different disturbance areas (Tokeshi 1993).

For each of the sites rare species was identified as the 25% least abundant species (see Gaston 1994), where as typical species contributed to the first 50% of the similarity within sites (Clarke & Warwick 1994).

Hierarchical agglomerative clustering with group-average linking was based on Bray-Curtis similarity measures using PRIMER v4.0 1994 (Clarke & Warwick 1994). Non-metric multidimensional scaling (MDS) was used to map site inter-relationships in an ordination of a specified number of dimensions (Kruskal & Wish 1978, Clarke 1993). Assessment of differences between sites was based on the program ANOSIM (analysis of similarity) from a calculated Bray-Curtis similarity matrix (Clarke & Green 1988).

Results

The relatively undisturbed sites had the highest bird species richness and diversity. There was no difference in species richness or diversity of the intermediate and severely disturbed areas (Table 12, Fig. 9). Bird density increased with a decrease in the level of disturbance (Table 12, Fig. 9). Values for the undisturbed areas showed greater evenness than other sites while they did not differ significantly between intermediate and severely disturbed areas (Table 12, Fig. 9).

The slopes of the rank-abundance curves decreased significantly with a decrease in the level of disturbance ($F=10.20$, $p<0.0001$, Fig. 10a). All the slopes deviated significantly ($p<0.001$) from zero. The intermediately disturbed area supported more rare species than the severely disturbed and undisturbed disturbed (Table 13 & Appendix 2).

Multidimensional scaling suggests three distinct assemblages along the disturbance gradient at a similarity of 40% (Fig. 11a-b, ANOSIM Global $R=0.78$, $p<0.05$).

The number of typical species declined gradually with an increase in disturbance regime (Table 14). Relatively undisturbed sites had more typical species than sites classified as intermediately disturbed areas. Most of the species typical of the intermediately disturbed sites were also occurred encountered in the disturbed and undisturbed areas (e.g. Yellowbreasted Apalis and Bleating Warbler). Also, each disturbance area contained at least one unique typical species (e.g. the Croaking Cisticola *Cisticola natalensis* was the only typical species recorded on severely disturbed sites within the intermediate area of disturbance).

Within the intermediate disturbed area species richness and diversity declined from least disturbed to the most severely disturbed sites (Table 15, Fig. 12). Density was the only parameter to peak at sites of intermediate regeneration age (Table 15, Fig. 12). Trends for evenness were not significantly different between different levels of disturbance (Table 15, Fig. 12).

The slopes of the rank-abundance curves decreased significantly with a decrease in the level of disturbance ($F=13.00$, $p<0.0001$, Fig. 10b). All slopes also deviated significantly ($p<0.001$) from zero. The number of rare species peaked at sites of intermediate regenerating, but was lowest on severely disturbed regenerating sites, followed by least disturbed regenerating sites (Table 16, Appendix 2).

Table 12: The mean \pm S.E. number of species, mean \pm S.E. total density ha^{-1} , mean \pm S.E. Shannon diversity, and mean \pm S.E. Pielou's evenness for bird assemblages as a function of different levels of habitat disturbances. Superscripts with different alphabetic letters associated with the mean values denote statistical significance between those sampling sites at $p < 0.05$. The Kruskal-Wallis test statistic is represented by H – values.

Level of disturbance	Study sites	Habitat type	Age of sampling site (years)	Number of transects surveyed	Mean \pm S.E. number of species ($H = 24.4$, $p < 0.001$)	Mean \pm S.E. total density ha^{-1} ($H = 29.2$, $p < 0.001$)	Mean \pm S.E. Shannon Diversity (J) ($H = 23.1$, $p < 0.001$)	Mean \pm S.E. Pielou's Evenness (E) ($H = 12.8$, $p < 0.01$)
Relatively undisturbed	Zulti /Sokhulu Mapelane	Diverse indigenous forest canopy & indigenous understorey	>50	13	17.3 ± 0.8^a	41.4 ± 4.5^a	2.6 ± 0.1^a	0.9 ± 0.0^a
Intermediately disturbed	Post-mined regenerating vegetation Unmined regenerating vegetation	Monoculture of woodland canopy & indigenous understorey	5 – 21	25	11.2 ± 0.6^b	35.2 ± 2.50^a	2.1 ± 0.1^b	0.9 ± 0.0^b
Severely disturbed	Neglected plantations Pine plantations Gum plantations	Exotic canopy of timber plantation trees & exotic understorey	30 - 40	15	11.2 ± 0.5^{bc}	14.2 ± 1.4^b	2.1 ± 0.1^{bc}	0.9 ± 0.01^{bc}

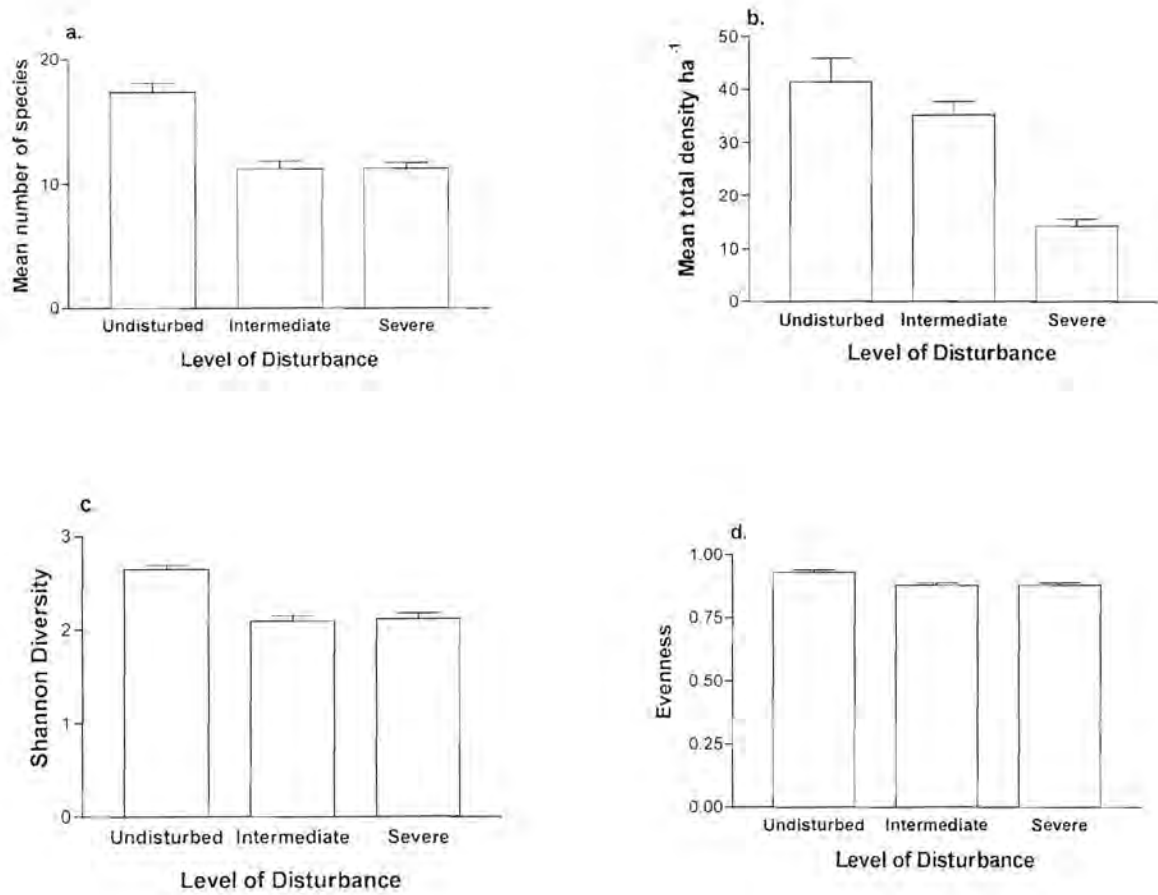


Figure 9: The mean number of species (a), mean total density ha^{-1} (b), Shannon diversity (c) and evenness (d) as a function of three different levels of habitat disturbances. The vertical lines denote a standard error of the mean values.

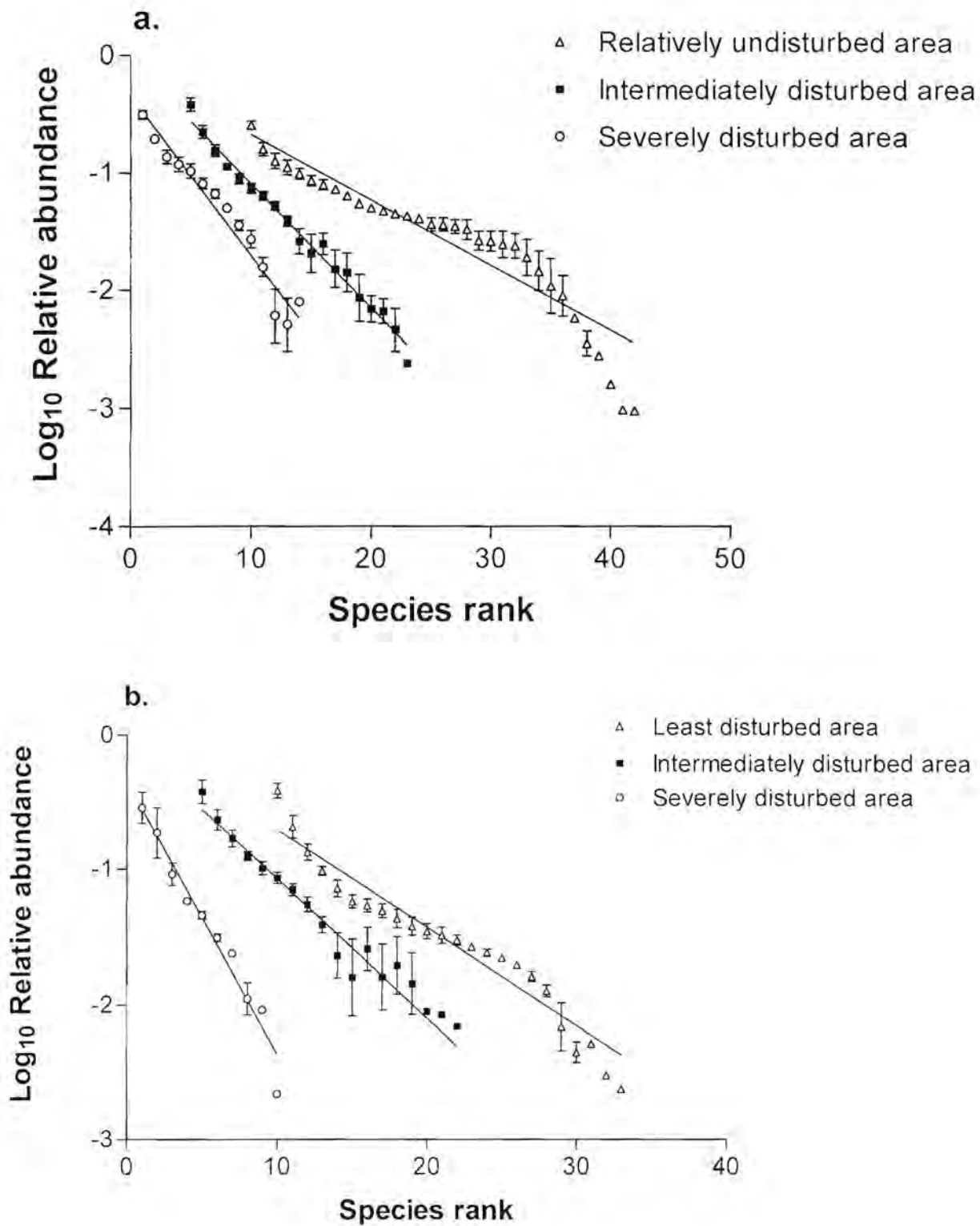


Figure 10: Rank-abundance curves for (a) bird assemblages as a function of three different levels of disturbance on the regional scale and (b) on the local scale for the intermediately disturbed area.

Table 13: The slopes of rank-abundance curves for bird assemblages and the number of rare species within each assemblage as a function of different levels of disturbances.

Level of disturbance	Study sites	Habitat type	Age of sampling site (years)	Slopes of rank-abundance curves	Number of rare species
Relatively undisturbed	Zulti /Sokhulu Mapeiane	Diverse indigenous forest canopy & indigenous understorey	>50	-0.09 ± 0.004	16
Intermediately disturbed	Post-mined regenerating vegetation Unmined regenerating vegetation	Monoculture of woodland canopy & indigenous understorey	5 - 21	-0.11 ± 0.004	29
Severely disturbed	Neglected plantations Pine plantations Gum plantations	Exotic canopy of timber plantation trees & exotic understorey	30 - 40	-0.14 ± 0.007	16

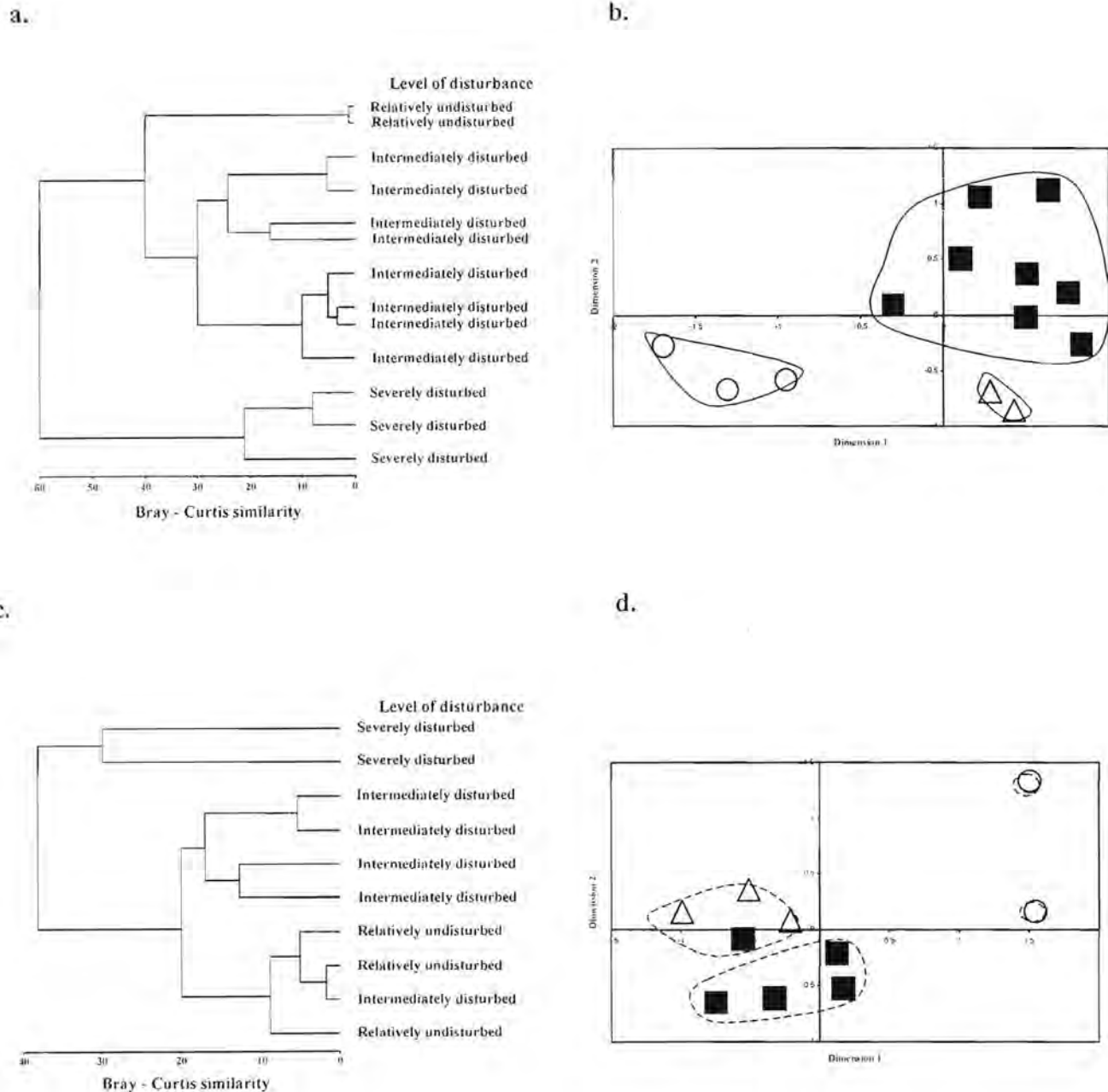


Figure 11: Dendrogram (a) and multi-dimensional scaling ordination (MDS, stress=0.09) (b) in two dimensions of the relative densities of species based on ranked Bray-Curtis similarities for three levels of disturbance. Dendrogram (c) and multi-dimensional scaling ordination (MDS, stress=0.09) (d) in two dimensions of the relative densities of species based on ranked Bray-Curtis similarities for three disturbance levels within intermediately disturbed area. \triangle - Relatively undisturbed area, \blacksquare - Intermediate disturbance area and \circ -Severely disturbed area.

Table 14: Typical bird species and their percentage contribution to mean within-site similarity for bird assemblages as a function of three different levels of disturbance. Only species contributing cumulatively 50% to the with-in site similarity are listed as typical species.

Level of disturbance	Study sites	Age of sampling site (years)	Species	Consistency	% Contribution
Relatively undisturbed	Zulti /Sokhulu Mapelane	>50	Yellowbellied Bulbul	8.36	11.11
			Bleating Warbler	5.43	9.19
			Yellowbreasted Apalis	11.39	10.10
			Natal Robin	7.4	8.48
			Terrestrial Bulbul	1.61	7.44
			Sombre Bulbul	22.81	10.52
			White-eared Barbet	33.11	10.52
Intermediately disturbed	Post-mined regenerating vegetation Unmined regenerating vegetation	5 - 21	Bleating Warbler	11.95	19.31
			Yellowbreasted Apalis	11.69	17.94
			Cape White-eye	6.27	14.77
			Squaretailed Drongo	12.94	11.32
			Lesser Masked Weaver	8.56	17.91
			Rattling Cisticola	5.68	17.45
Severely disturbed	Neglected plantations Pine plantations Gum plantations	30 - 40	Blackeyed Bulbul	10.08	22.00
			Rattling Cisticola	12.34	17.79
			Yelloweyed Canary	7.09	21.51
			Olive Sunbird	5.05	14.95
			Bleating Warbler	8.66	13.83

Table 15: The mean \pm S.E. number of species, mean \pm S.E. total density ha^{-1} , mean \pm S.E. Shannon diversity, and mean \pm S.E. Pielou's evenness for bird assemblages as a function of different levels of local disturbance within the area of intermediate disturbance. Superscripts with different alphabetic letters associated with the mean values denote statistical significance between those sampling sites at $p < 0.05$. The absence of superscripts refers to insignificant mean values between all sampling sites. The Kruskal-Wallis test statistic is represented by H – values.

Level of disturbance	Study sites	Habitat type	Age of sampling site (years)	Number of transects surveyed	Mean \pm S.E. number of species ($H=11.1, p<0.01$)	Mean \pm S.E. total density ha^{-1} ($H=20.9, p<0.001$)	Mean \pm S.E. Shannon Diversity (J) ($H=9.8, p<0.01$)	Mean \pm S.E. Pielou's Evenness (E) ($H=1.9, p>0.05$)
Least disturbed	Post-mined regenerating vegetation	Monoculture of woodland canopy & indigenous understorey	15 - 21	9	12.7 ± 0.7^a	26.7 ± 1.5^a	2.3 ± 0.1^a	0.9 ± 0.0
	Unmined regenerating vegetation							
Intermediately disturbed	Post-mined regenerating vegetation	Monoculture of woodland canopy & indigenous understorey	5 - 14	16	10.4 ± 0.8^{ab}	39.9 ± 3.3^a	2.0 ± 0.1^{ab}	0.9 ± 0.0
	Unmined regenerating vegetation							
Severely disturbed	Post-mined regenerating vegetation Cape Vidal/St.Lucia	Grassland	1-4 but Cape Vidal unknown	8	7.9 ± 0.7^b	9.0 ± 3.3^b	1.7 ± 0.1^b	0.8 ± 0.0

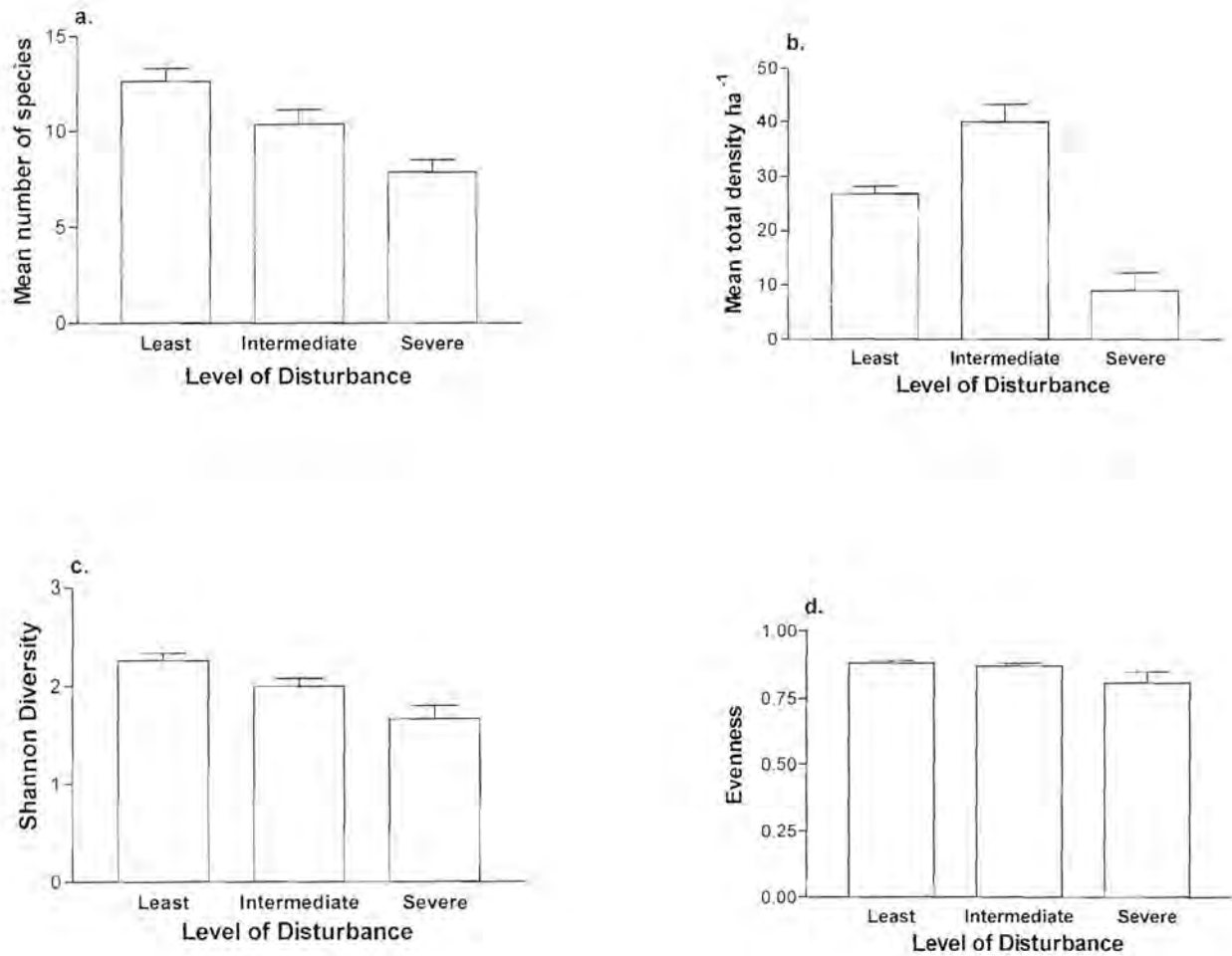


Figure 12: The mean number of species (a), mean total density ha^{-1} (b), Shannon diversity (c) and evenness (d) as a function of three different levels of local disturbances within the intermediately disturbed area. The vertical lines denote a standard error of the mean values.

Table 16: The slopes of rank-abundance curves and the number of rare species on each level of disturbance within the area of intermediate disturbance.

Level of disturbance	Study sites	Habitat type	Age of sampling site (years)	Slopes of rank-abundance curves	Number of rare species
Least disturbed	Post-mined regenerating vegetation Unmined regenerating vegetation	Monoculture of woodland canopy & indigenous understorey	15 - 21	-0.103 ± 0.006	14
Intermediately disturbed	Post-mined regenerating vegetation Unmined regenerating vegetation	Monoculture of woodland canopy & indigenous understorey	5 - 14	-0.107 ± 0.006	20
Severely disturbed	Post-mined regenerating vegetation Cape Vidal/St.Lucia	Grassland	1 - 4 but Cape Vidal unknown	-0.202 ± 0.012	8

Multidimensional scaling of the assemblages within the intermediate disturbance area showed less clear clustering (Fig. 10 c-d, ANOSIM Global $R=0.613$ $p<0.05$), but three distinct assemblages from each disturbance regime clustered at a lower similarity (20%), with the incorporation of one intermediately disturbed site (aged 12-14 years) with the least disturbed sites (Fig. 11c). The assemblages on severely disturbed sites appear to be more distinct than the rest of the species compositions within the intermediately disturbed area (Fig. 11c). Here the number of typical species also increased with an increase in regeneration age (Table 17).

Discussion

The effect of disturbance on diversity

Disturbance is considered one of the main processes responsible for diversity patterns across landscapes (Huston 1994). Most published relationships between disturbance and diversity predict that the highest diversity should occur at intermediate levels of disturbance (e.g. Miller 1982, Petraitis *et al.* 1989). Others conclude that this relationship depends on whether the organisms involved are terrestrial or mobile (Fuentes & Jacsić 1988). Based on my analysis it was clear that bird communities on coastal dune vegetation lend little support to the intermediate disturbance hypothesis (Petraitis *et al.* 1989, Mackey & Currie 2000) for all measured community parameters. The exception was for density at a local scale within the intermediate disturbed area. All community variables peaked in relatively undisturbed areas and decreased with increased disturbance.

Fuentes & Jacsić (1988) suggest that the failure for diversity parameters to increase at intermediate disturbance regimes may not be a general phenomenon for land animals but more applicable for intertidal organisms and terrestrial plants. They suggested three conditions necessary for such an increase in species diversity at intermediate disturbances; namely (1) a continual release of resources; (2) a large species pool for recolonisation, and (3) strong interspecific competition among these colonists. They concluded that the pattern was unsuitable for terrestrial animals (Fuentes & Jacsić 1988, Petraitis *et al.* 1989). Of these conditions only the second may be upheld for the increase in density recorded during the current study at intermediate levels of disturbance on a local scale (intermediate disturbance area). Large undisturbed areas to the north of this area may act as a species pool for the colonisation of regenerating sites. In addition, the frequency and size of the disturbance will

Table 17: Typical species and their percentage contribution to mean within-site similarity for three different levels of disturbance within the intermediate disturbance area. Only species contributing cumulatively 50% to the with-in site similarity are listed as typical species.

Level of disturbance	Study sites	Age of sampling site (years)	Species	Consistency	% Contribution
Least disturbed	Post-mined regenerating vegetation	15 - 21	Bleating Warbler	15.82	17.23
			Yellowbreasted Apalis	14.12	15.48
	Cape White-eye		6.27	14.77	
	Unmined regenerating vegetation		Squaretailed Drongo	12.94	11.32
Intermediately disturbed	Post-mined regenerating vegetation	5 - 14	Yellowbreasted Apalis	6.83	22.85
			Bleating Warbler	9.45	20.71
	Unmined regenerating vegetation		Lesser Masked Weaver	8.56	17.91
	Rattling Cisticola		5.68	17.45	
Severely disturbed	Post-mined regenerating vegetation Cape Vidal/St.Lucia	1-4 but Cape Vidal unknown	Rattling Cisticola	5.38	36.58
			Croaking Cisticola	10.84	31.21

also affect the magnitude of the observed increase in species diversity (Miller 1982). Some sites within the intermediate disturbance area are under frequent disturbance which may have a negative impact on species diversity. These include annual burning for grazing (as in the case at the Cape Vidal/St. Lucia grasslands), cattle grazing and clearcutting for wood (Weisser 1980, Lubke *et al.* 1992).

The results illustrate that diversity decreased linearly (negative monotonically) from relatively undisturbed forests to severely disturbed areas such as those sites dominated by exotic plantations. The same pattern was identified on a local scale, for which diversity was only measured along disturbance regimes on regenerating vegetation (see Table 13). Here the measured diversity was the greatest on the oldest regenerating sites (woodlands) and least on the youngest sites (grasslands).

The results also confirm Mackey & Currie's (2000) findings that the relationship between richness and disturbance are not consistent, even over large disturbance regimes. They hypothesize that the peak in diversity at intermediate levels of disturbance is more subtle and only recorded occasionally. They conclude that the diversity-disturbance relationship depends more on sampling intensity than disturbance effects and illustrate that the diversity-disturbance relationship follows more closely a monotonic function than a peaked function of disturbance. My sampling methods were non-exhaustive but covered each sampled site intensively, such that I am confident most rare species should have been detected. This could explain the greater number of species recorded from undisturbed and climax sites than areas of intermediate disturbance in this study.

Several other factors, including spatial heterogeneity (Roth 1976, Cody 1981, Rotenberry 1985, Kritzing 1996) and stability (Pimm 1986, Bowers & Harris 1994, Tilman & Downing 1994, Tilman 1997) may explain why diversity measures were higher on undisturbed areas than the rest of the study site. It has long been known that vertical and horizontal stratification of plant diversity influence the habitat choice of bird species (Kritzing 1996). Most studies on bird communities have shown that diversity tends to be the highest and most even in areas such as mature forest that contain more habitats in this study site (the undisturbed forests) and more species are supported than in other habitats (Wiens 1989, Rosenszeig 1992, Schluter & Ricklefs 1993). Therefore the undisturbed and mature dune forests, as well as the oldest regenerating sites on a local scale, may support more diverse plant communities. This may explain the

higher numbers of bird species in these areas while the inverse is true for severely disturbed areas such as neglected plantations and grasslands.

The effect of disturbance on species composition

Disturbance events not only influence species diversity, but should affect species composition (Wiens 1989, Cole & Landras 1996). Therefore, major disturbance events such as mining should have major conservation implications for certain species as rare or endemic species could become locally extinct. The intermediate disturbance hypothesis predicts that those species found at intermediate disturbance regimes, such as the regenerating sites, should represent a combination of pioneers (or secondary successional species) coexisting with forest specialist species (Miller 1982, Dial & Roughgarden 1997). I did not find this, as the typical species encountered on the regenerating sites were shared between all the other sites within the study area. At a local level, the number of typical species increased linearly from youngest to the oldest aged sites, while the middle-aged sites did not harbour more typical species. The species dominance was also greatest on the grassland sites and lowest (most even) on the oldest of the regenerating sites. This may explain the observed decrease in typical species with a decrease in the age of sites. Grassland sites also contained one dominant species whilst the oldest sites contained a greater number of species at more even distributions.

From the ordination data it was clear that each disturbance area were occupied by different species assemblages. Many authors have explained the difference in bird communities through differences in vegetation structure (e.g. Cody 1981, Rotenberry 1985, Wiens 1989) rather than disturbance *per se*. For example, the exotic plantation sites supported bird assemblages different to those of the other two disturbance areas. Here habitat generalist species such as Blackeyed Bulbul (Hart 1997) occurred more commonly than habitat specialists. Others, such as Yelloweyed Canary feeding on pine seeds and Olive Sunbird on bluegum nectar (Maclean 1993, Nuttal 1997) have adapted to exploit the abundant resources not available to more specialised species typical of forest and woodland interiors (Cole & Landras 1996). Also, the bird assemblages on the severely disturbed regenerating sites (such as cisticolas) are species which prefer grassland to woodlands. The same is true for undisturbed forest specialists, as these are hole-nesters (e.g. Trumpeter Hornbill *Bycanistes bucinator*, White-eared Barbet *Stactolaema leucotis*) and frugivores (e.g. Blackbellied Starling

Lamprotornis corruscus) which depend on the presence of large fruiting trees such as fig trees of the genus *Ficus*.

Compared to sites of the other two disturbance areas, the sites in the intermediately disturbed area had more rare species. The difference in the number of rare species between the three disturbance regimes within the intermediate disturbance area were not significant. Such diffusive rarity, as described by Gaston (1994), is relatively common in local scale studies such as this one. Similar results have also been recorded from studies on other taxa (Van Rensburg *et al.* 1999). In this study certain bird species might occur at the edge of their distribution range (e.g. Cape Canary *Serinus canicollis*, Nuttal 1997) or in unsuitable habitats (e.g. Narina Trogon *Apaloderma narina* and Tambourine Dove *Turtur tympanistris*, Harrison 1997) while others are recorded as transients (Brown 1984, Gaston *et al.* 1993, Brown *et al.* 1996, Gaston 1993). These would include most of the locally rare species occurring in the regenerating area such as Squaretailed Drongo and Yellowspotted Nicator *Nicator gularis*. Also, none of the species considered rare in the present study were geographically rare in southern Africa, though the Palecrowned Cisticola *Cisticola brunnescens* from the grasslands of Cape Vidal/St. Lucia can be considered vulnerable (Brooke 1984) while Rudd's Apalis is restricted (endemic) to undisturbed forest of Maputaland (Harrison *et al.* 1997). Both areas where these species occur are maintained as grasslands through regular man made interferences atypical for coastal dune forests such as burning and grazing.

I conclude that bird communities on coastal dune vegetation do not support the intermediate disturbance hypothesis. Also, the bird communities of northern KwaZulu-Natal follow a general linear monotonic trend with highest diversity and evenness found at undisturbed areas and not on intermediate disturbed sites. Thus I argue that habitat heterogeneity may have a stronger effect on the observed patterns than disturbance. I must add that birds are highly mobile species, while most studies (see Mackey & Currie 2000) examining the intermediate disturbance hypothesis have considered more sessile communities. Therefore, bird communities in general may rarely support the intermediate disturbance hypothesis, at least at relatively small regional and local spatial scale at which I examined them. Only further long term monitoring of regenerating vegetation will provide further insight on the validity of the intermediate disturbance hypothesis for bird assemblages and the effect that disturbance might have on true rare species of northern KwaZulu-Natal, South Africa.

Chapter 5

The contribution of regenerating coastal dunes towards regional bird diversity

Introduction

Brown (1984) maintained that bird species with wider distributions should occupy more habitats than species with narrower distributions. Therefore, rare species tend to be more habitat-specific than common and widespread species (Brown *et al.* 1996). Studies have also shown that regional areas tend to be more species rich than local areas (MacArthur & Wilson 1967, Ricklefs 1987). This increase in species richness on a regional scale may be the result of the greater surface area and therefore availability of habitat types (MacArthur & Wilson 1967, Ricklefs 1987).

The region along the coast north of Richards Bay is dominated by a mosaic of patches of indigenous vegetation at different stages of recovery from disturbances, including slash-and-burn agriculture and afforestation with exotic species. Some of these patches of natural vegetation are being invaded by a variety of exotic plant species, while others appear to be relatively pristine, with a high conservation potential. Other patches in the region comprise plantations of exotic species maintained for commercial purposes. Common exotics include beefwood, *Casuarina equisetifolia* (J.R. & G.Forster), cultivated for a charcoal industry, as well as pines, *Pinus elliotii* (L.) and bluegum, *Eucalyptus grandis* (L'Her), for paper pulping and pylon poles. Overgrazing and/or fire in other areas, including some within designated conservation areas, are giving rise to sites within the region being maintained as grasslands (Weisser 1980).

These disturbed patches, together with the patches of vegetation resulting from post-mining dune rehabilitation may have consequences for bird diversity, either by providing habitats atypical for the region and/or by changing the relative ratios of disturbed to undisturbed habitats typical of regions with only minimal human disturbance (see Chapter 4). This may result in the establishment of species atypical of the region. Though a habitat disturbance-recovery cycle may enhance bird diversity in the region, the relatively high incidence of

disruption and fragmentation may have a negative impact on diversity by affecting rare species, which typically occur at low abundances (Cole & Landras 1996, MacNally 1997). The post-mined regenerating areas along the coast could house bird assemblages atypical of the region, making the rehabilitation of coastal dune forests at variance with conservation ideals.

The regenerating coastal dune vegetation north of Richards Bay, KwaZulu-Natal, harbours a variety of bird species (see Appendix 1). In an effort to determine the consequences of dune rehabilitation for bird assemblages, this chapter compares the bird community of the region including that of the rehabilitating dunes, with that of the local region excluding the dunes area.

Material and Methods

Study sites included in this analysis comprise post-mined regenerating sites (six sites of a known age from the summer (1 December to 22 December) database of 1998/99, the relatively undisturbed mature forests (Mapelane and Zulti/Sokhulu), severely disturbed afforested areas (pine, gum and beefwood plantations), unmined sites of coastal dune indigenous woodland (three sites) and the Cape Vidal/St. Lucia grasslands as defined in Chapter 2.

Hierarchical agglomerative clustering with group-average linking was performed on the data for each sampled site based on Bray-Curtis similarity measures using PRIMER v4.0 1994 (Clarke & Warwick 1994) as described in Chapter 2. Subsequently, non-metric multidimensional scaling (MDS) was used to map site inter-relationships in an ordination of a specified number of dimensions (Kruskal & Wish 1978, Clarke 1993). Any differences between the assemblages were tested using the program SIMPER (analysis of similarity) (Clark & Green 1988).

For each species assemblage, rarefaction and rank-abundance curves were constructed, using non-metric multidimensional ordination as described by James & Rathbun (1981) and Tokeshi (1993). Least-squares regression analyses fitted to the rank-abundance curves to enable a comparison of slopes between the assemblages for equitability (Tokeshi 1993).

The mean number of species (S), the mean number of rare species (the 25 % least abundance species (Gaston 1994)), and the mean number of unique species were calculated for each of the assemblages (differences in values between assemblages were tested by using the Kruskal-Wallis one-way analyses of ranks and Dunn's distribution-free multiple range test

(Sokal & Rohlf 1995)). Typical species were determined for each assemblage as described in Chapter 3.

To quantify the potential affect of the rehabilitating sites on the bird assemblages of the region, macro community (species diversity, richness and evenness) and compositional characteristics were calculated for the entire region, both including and excluding the data from the post-mined regenerating sites. Differences in values between assemblages were tested using Kruskal-Wallis one-way analyses of ranks and Dunn's distribution-free multiple range test (Sokal & Rohlf 1995).

Results

Based on the non-metric multidimensional scaling, four assemblages could be distinguished for the region (ANOSIM Global $R = 0.791$, $p < 0.05$, Fig. 13). These included separate assemblages for each of the two grassland sites (Cape Vidal/St. Lucia and the 1-4 year old regenerating site), an assemblage for all the sites dominated by exotic plantations and an assemblage for all other sites (indigenous regenerating sites >5 years old plus mature forests).

The greatest number of expected species was recorded on indigenous coastal dunes comprising forest and regenerating vegetation (Assemblage 1, Table 18). Exotic plantations included the second highest expected number of species (Assemblage 2, Table 18) while the 1-4 year old regenerating grassland included the lowest number of expected species (Assemblage 4, Table 18).

Slopes of the rank-abundance curves for the assemblages differed significantly from each other ($F=28.58$, $p < 0.0001$) and from zero ($p < 0.001$) (Table 19). The slopes for the assemblage on the mined regenerating grassland (Assemblage 4) and for the grasslands of Cape Vidal/St. Lucia (Assemblage 3) were significantly steeper than those for the other two assemblages (Table 19). The slopes for the two grassland assemblages also differed significantly from each other. The slope for areas dominated by exotic plantations (Assemblage 2) was also steeper than that for the indigenous woodland areas (Assemblage 1) (Table 19).

Species richness was greatest for the assemblages on indigenous sites (Assemblage 1, Table 20), followed by assemblages on exotic plantations (Assemblage 2, Table 20). The two grassland assemblages had the lowest incidence of species richness (lower on the regenerating grassland of 1-4 years old) (Assemblages 3 & 4, Table 20). Differences between the number of

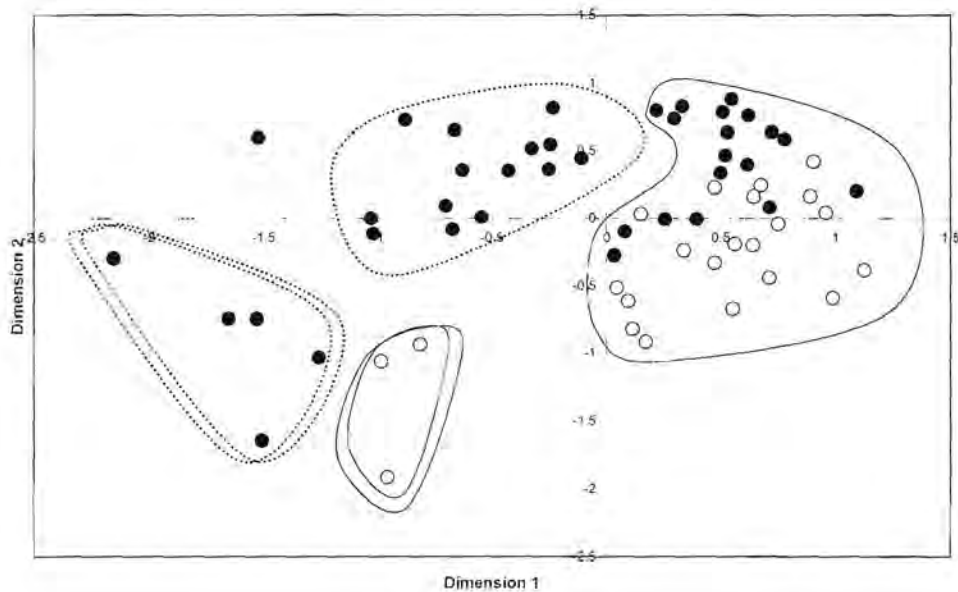


Figure 13: Two-dimensional non-metric multidimensional scaling ordination of the relative densities of species based on ranked Bray-Curtis similarities of the bird assemblages on regenerating and regional sites (stress = 0.17). Regional unmined sites (●) and post-mined regenerating sites (○). Each symbol represents the value for a transect. The double solid lines represent an assemblage on grasslands of 1-4 years old and the double dashed lines represent an assemblage on grasslands at Cape Vidal/St. Lucia. The dashed lines encircle symbols based on values from neglected, pine and gum plantations. The solid lines encircle symbols based on values from regenerating indigenous woodlands and from forests. The double dashed lines encircle disturbed grasslands while the double solid lines enclose transitional grassland.

Table 18: The mean \pm S.E. observed number of species and mean \pm S.E. expected number of species at 30 individuals obtained from rarefaction curves for four bird assemblages identified from non-metric multidimensional scaling of all sites.

Sampling area	Number of transect lines surveyed	Observed number of species (mean \pm S.E.)	Expected number of species (mean \pm S.E.)
Assemblage 1 (Coastal dune forest, woodland and regenerating vegetation)	38	13.29 \pm 0.66	12.0 \pm 1.2
Assemblage 2 (Exotic plantations)	15	11.20 \pm 0.46	10.9 \pm 0.6
Assemblage 3 (Cape Vidal/St. Lucia grasslands)	5	8.60 \pm 0.51	6.0 \pm n/a
Assemblage 4 (Regenerating grasslands of 1-4 years old)	3	6.67 \pm 1.33	5.0 \pm n/a

Table 19: The slopes of rank-abundance curves for each assemblage obtained from non-metric multidimensional scaling of all sites. The slopes were calculated using least square regression analyses of log transformed abundance values.

Sampling area	Slopes of rank-abundance curves (mean \pm S.E.)	R ²	F - value	p - value
Assemblage 1 (Coastal dune forest, woodland and regenerating vegetation)	-0.007 \pm 0.002	0.77	1674	< 0.0001
Assemblage 2 (Exotic plantations)	-0.099 \pm 0.004	0.81	723.9	< 0.0001
Assemblage 3 (Cape Vidal/St. Lucia grasslands)	-0.144 \pm 0.011	0.80	168.7	< 0.0001
Assemblage 4 (Regenerating grasslands of 1-4 years old)	-0.196 \pm 0.017	0.86	140.3	< 0.0001

Table 20: The mean \pm S.E. species richness, the mean \pm S.E. of rare species and the mean \pm S.E. of unique species for each assemblage obtained from non-metric multidimensional scaling. Superscripts with different alphabetic letters denote statistical differences between the assemblages after using a Kruskal-Wallis test.

Sampling area	Species richness (mean \pm S.E.) $H^* = 15.20, p < 0.05$	Number of rare species (mean \pm S.E.) $H^* = 5.18, p > 0.05$	Number of unique species (mean \pm S.E.) $H^* = 4.32, p > 0.05$
Assemblage 1 (Coastal dune forest, woodland and regenerating vegetation)	13.29 \pm 0.66 ^a	5.60 \pm 0.64	1.20 \pm 0.59
Assemblage 2 (Exotic plantations)	11.20 \pm 0.46 ^a	6.67 \pm 0.67	1.33 \pm 0.33
Assemblage 3 (Cape Vidal/St. Lucia grasslands)	8.60 \pm 0.51 ^b	5.0 \pm n/a	8.0 \pm n/a
Assemblage 4 (Regenerating grasslands of 1-4 years old)	6.67 \pm 1.33 ^b	3.0 \pm n/a	2.0 \pm n/a

* Kruskal-Wallis test statistic

rare species for each assemblage was not significant, although the exotic plantation assemblage tended to include more rare species (Assemblage 2, Table 20), while the post-mined regenerating grassland included the least number of rare species (Assemblage 4, Table 20). The grassland sites incorporated the most unique species for the region, especially on the Cape Vidal/ St. Lucia grasslands, although differences were not significant (Assemblage 3, Table 20).

Three typical species (Bleating Warbler, Blackeyed Bulbul and Yellowbellied Bulbul) were identified for the region (Table 21). The most typical species on the indigenous coastal dune assemblages (Assemblage 1) were the Bleating Warbler and Yellowbellied Bulbul. In addition five species were identified as typical on the mature coastal dune forests site (see Table 14, Chapter 4), though only two of these (Yellowbreasted Apalis and Natal Robin) contributed throughout these sites.

For mature coastal forests at Mapelane four species were identified as typical, of which two (White-eared Barbet and Sombre Bulbul) contributed throughout individual sites (see Table 14, Chapter 4). At Cape Vidal/St. Lucia (Assemblage 3), the most typical species was the Croaking Cisticola, while at the 1-4 year old regenerating site (Assemblage 4) this was replaced by Rattling Cisticola (Table 21). The most typical species on the exotic plantations (Assemblage 2) were the Blackeyed Bulbul and Bleating Warbler.

The contribution of bird assemblages of rehabilitating dunes to regional diversity

Non-metric multidimensional scaling illustrated three distinct assemblages (Fig. 14, ANOSIM Global $R=0.78$, $p<0.05$), once information collected from the post-mined regenerating sample sites had been excluded from the analysis. The Cape Vidal/St. Lucia assemblage (Assemblage 3) remained distinct from other assemblages. Exotic plantation sites formed the second assemblage (Assemblage 2), while the mature forest and other unmined sites constituted the third species assemblage (Assemblage 1, Fig. 14).

Species richness was highest on the assemblages occurring on unmined indigenous vegetation (Assemblage 1, Table 22) and lowest on the Cape Vidal/St. Lucia grassland assemblage (Assemblage 3, Table 22). The number of rare species occurring on each assemblage did not differ significantly, although values were higher for exotic plantation

Table 21: Typical species and their percentage contribution to mean within-site similarity for the whole region and four assemblages obtained from non-metric multidimensional scaling. Only species contributing cumulatively 50% to the within site similarity were listed as typical species.

Sampling area	Species	Consistency	% Contribution
Regional (all sites included)	Bleating Warbler	1.43	19.33
	Blakeyed Bulbul	1.00	12.52
	Yellowbellied Bulbul	0.82	10.54
Assemblage 1 (Coastal dune forest, woodland and regenerating vegetation)	Bleating Warbler	3.12	20.23
	Yellowbellied Bulbul	3.54	18.00
Assemblage 2 (Exotic plantations)	Blackeyed Bulbul	6.42	22.89
	Bleating Warbler	2.33	15.26
Assemblage 3 (Cape Vidal/St. Lucia grasslands)	Croaking Cisticola	9.26	29.95
Assemblage 4 (Regenerating grasslands of 1-4 years old)	Rattling Cisticola	6.42	36.10

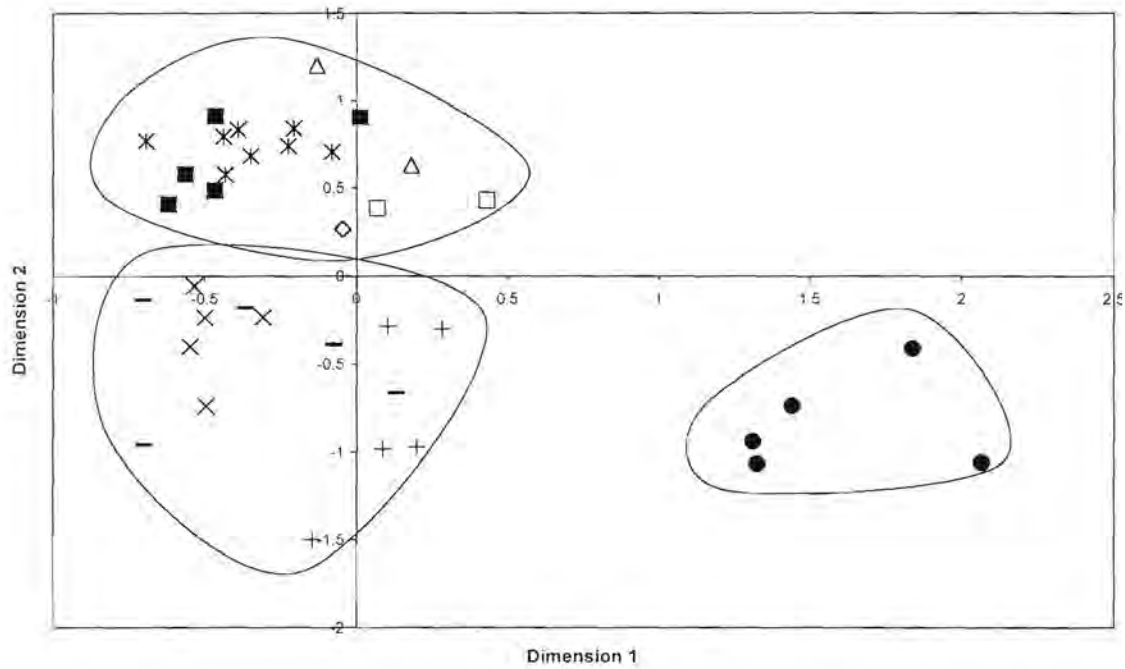


Figure 14: Two-dimensional non-metric multidimensional scaling ordination of the relative densities of species based on ranked Bray-Curtis similarities of the bird assemblages (stress = 0.14). (● denote Cape Vidal/St. Lucia site, □ 5-8 year old unmined site, △ 9-11 year old unmined site, ◇ 19-21 year old unmined site, ■ Mapelane site, ✖ Zulti/Sokhulu site, + neglected plantations, - pine plantations and × gum plantations. Each symbol represents the value for a transect.

Table 22: The mean \pm S.E. species richness, the mean \pm S.E. of rare species and the mean \pm S.E. of unique species for each assemblage obtained from non-metric multidimensional scaling after removal of data from the post-mined regenerating area. Superscripts with different alphabetic letters denote statistical differences between the assemblages after using a Kruskal-Wallis test.

Sampling area	Species richness (mean \pm S.E.) $H^* = 22.99, p < 0.0001$	Number of rare species (mean \pm S.E.) $H^* = 1.17, p > 0.05$	Number of unique species (mean \pm S.E.) $H^* = 3.13, p > 0.05$
Assemblage 1 (Coastal dune forest and unmined woodland)	16.39 \pm 0.78 ^a	6.60 \pm 1.08	1.60 \pm 1.12
Assemblage 2 (Exotic plantations)	11.20 \pm 0.46 ^b	6.67 \pm 0.67	1.33 \pm 0.33
Assemblage 3 (Cape Vidal/St. Lucia grasslands)	8.60 \pm 0.51 ^b	5.0 \pm n/a	8.0 \pm n/a

* Kruskal-Wallis test statistic

Table 23: The results of the rank-abundance curves for three assemblages (without the inclusion of data from the post-mined regenerating sites) obtained from non-metric multidimensional scaling. The slopes were calculated using least square regression analyses of log transformed abundance values.

Sampling area	Slopes of rank-abundance curves (mean \pm S.E.)	R ²	F-value	p-value
Assemblage 1 (Coastal dune forest and unmined woodland)	-0.062 \pm 0.002	0.84	1557	< 0.0001
Assemblage 2 (Exotic plantations)	-0.099 \pm 0.004	0.81	723.9	< 0.0001
Assemblage 3 (Cape Vidal/St. Lucia grasslands)	-0.144 \pm 0.011	0.80	168.7	< 0.0001

assemblages (Assemblage 2, Table 22). Similarly, the number of unique species did not differ significantly, though figures were highest for the Cape Vidal/St. Lucia grassland assemblage (Assemblage 3, Table 22).

The slopes of the rank-abundance curves differed significantly from each other for the three assemblages ($F=30.51$, $p<0.0001$) and from zero ($p<0.0001$). Slopes for the assemblages on indigenous forest and unmined woodland (Assemblage 1) were shallower than the other two assemblages, while the grassland assemblage had the steepest slope (Assemblage 3, Table 23). All assemblages (Assemblage 1, 2 & 3) harboured the same typical species (Table 21). A comparison of the assemblages, both including and excluding data from the rehabilitating sites, revealed that none of the measured values of the slopes obtained from rank-abundance curves, species richness, rare species, unique species or species composition differed obviously from each other.

Discussion

With the inclusion of information collected from the rehabilitating sites four distinct bird assemblages could be identified for the region (see Fig. 13). These assemblages occur on three broadly defined habitats (sites); namely grasslands, exotic plantations, indigenous woodlands and coastal forests. The exclusion of data from the rehabilitating sites reduced the number of assemblages to three, these still representing the habitat types referred to above. From this it may be deduced that habitat rehabilitation created a habitat type atypical for the region, through a grassland. However, the grasslands on rehabilitating dunes are transient, developing into transient scrublands within five years of their establishment, a habitat-type which also occurs in sites that have not been exposed to rehabilitation.

The assemblages of the regenerating post-mined and other unmined sites clustered with those of the mature forest sites. These areas contain high bird diversity, with only a few dominant species on the mature dune forest, in contrast to areas of exotic vegetation and grasslands (Cape Vidal/St. Lucia and the 1-4 year old site) which exhibit lower bird diversities and a greater number of dominant species. It is not unusual to find fewer species on disturbed sites (such as sites invaded by exotic vegetation) or areas dominated by grasslands. Factors forcing this trend are discussed in Chapter 3 (pages 50-53).

Grassland sites are colonised by early-successional species (pioneer species, such as cisticolas), all with relatively low body masses (13-22 grams, Maclean 1993), large clutch sizes (mean of 3.3 eggs, Maclean 1993) and shorter fledging periods (more than one clutch reared per season, 14 days per clutch, Smith & MacMahon 1981, May 1984, Mönkkönen & Helle 1987, Maclean 1993). Several authors have succeeded in explaining, using the life-history traits of species, why certain species occur on disturbed areas while others prefer areas with minimal or no disturbance (e.g. May 1984, Mönkkönen & Helle 1987, Wiens 1989, McCook 1994, Pacala & Rees 1998). Others have predicted that vegetation structure shapes the different species composition observed in the different habitats (MacArthur 1964, MacArthur *et al.* 1966, James & Wamer 1982, Erdelen 1984). Therefore, in my present study I would expect that mature forests of the identified indigenous assemblage (e.g. Mapelane with large, dead and fruiting tree species (Venter 1976)) should attract frugivores (e.g. Sombre Bulbuls) and hole-nesters (e.g. White-eared Barbets). The presence of a well-developed understorey in this habitat (see Weisser 1980, Kritzinger & van Aarde 1998) should attract understorey specialists such as species like Natal Robin and Terrestrial Bulbul.

In the present study the bird assemblage of the exotic plantations consists of fewer species than the assemblage occurring on indigenous vegetation (Assemblage 1); here the vegetation type was distinct from other vegetation patches in the region. Most species occurring on non-native habitats were expected to be generalists (Cole & Landras 1996). Some bird species typical of patches of timber plantations are similar through southern Africa, where they occupy a range of habitats (e.g. Blackeyed Bulbul, Keith *et al.* 1992, Hart 1997). Others, such as Yelloweyed Canary which may feed on pine seeds, or Olive Sunbird which feed on the nectar of gum flowers (Cyrus & Robson 1980, Irwin 1981, Parker 1991, Nuttall 1997), appear to have adapted to a vacant niche and abundant resource available in these patches.

Brown (1984) hypothesized that generalist species tend to occur over a wide range of habitats. Therefore, the typical species for the region (e.g. the Blackeyed Bulbul, Bleating Warbler, Yellowbellied Bulbul) all share a broad easterly distribution within southern Africa (Harrison *et al.* 1997, Maclean 1993). According to Brown's (1984) hypothesis, these species should be locally common and widespread. The most typical (common) species was the Blackeyed Bulbul, which is considered by Keith *et al.* (1992) to be the most widespread and abundant bird species in Africa. Hart (1997) showed that this species is most abundant in

KwaZulu-Natal. These typical (common) species would attain higher abundances at the centre of their distributional range (the study area is a stronghold for most typical species) and occur at lower abundance at the margins of their distribution (Gaston 1994). The localised (rare species, Appendix 2) species have incomplete geographic ranges and are more specialised in their habitat preference. As such rare species may be at risk of becoming locally extinct and being recolonised by other more widespread species. This pattern would follow the typical dynamics predicted by a metapopulation model (Hanski 1982, Hanski & Gyllenberg 1993, Hanski *et al.* 1993). The bird assemblages on the coastal dunes of northern KwaZulu-Natal may conform to a metapopulation model, with much generalisation on the structuring of the communities involved.

The number of rare and unique species identified for the local bird assemblage (Assemblage 1) was not affected by the exclusion of information from the rehabilitating sites. Although unique species can be considered as endemic on their recorded sites, these records were not consistent (therefore not significant) in their abundance throughout the region. Therefore, the six unique species thought to be endemic for the post-mined regenerating area (Cuckoo Hawk *Aviceda cuculoides*, Cardinal Woodpecker *Dendropicos fuscescens*, Diederik and Emerald Cuckoo *Chrysococcyx caprius* and *C. cupreus*, Dusky Flycatcher and Fantailed Cisticola) cannot be regarded as such due to their inconsistent abundances. Their distributions in the study area could be ascribed to their catholic preference towards any particular habitat (e.g. dune forest or *Acacia* thornveld) without high site fidelity, except for the cisticola that occupies grassland (Maclean 1993, Harrison 1997). These species can occur in any dense habitat structure (as in the case of the woodland structure found on the regenerating sites) and, in the case of the two cuckoos, depending on the abundance of their hosts (weavers and the Bleating Warbler).

Also, none of the species considered rare in the present study are considered to be geographically rare in southern Africa, although the Palecrowed Cisticola from Cape Vidal/St. Lucia may be considered vulnerable (see Chapter 4). Species compositions for the region differed only for the grasslands, with the inclusion of an additional assemblage (Assemblage 4) inhabited by Rattling Cisticola.

Bird species typical of the post-mined regenerating areas occurred on all other unmined sites (see the ordination, Fig. 13). However, some species typical of the unmined region (see

Table 21 and Table 14, Chapter 4) were not typical of the post-mined regenerating area. Many of the species typical of the unmined indigenous sites in the region (such as Natal Robin, Terrestrial Bulbul and White-eared Barbet) are habitat specialists with preferences for large dead trees, fruiting trees and a well developed terrestrial plant layer (see Chapter 3).

It may be concluded that bird communities on post-mined regenerating coastal dunes do not include rare species, endemics or species of special conservation concern, such as threatened or endangered species. These communities do not appear to alter the bird community structure and species composition of local assemblages in the region. Therefore, I conclude that the post-mined rehabilitation of bird communities in KwaZulu-Natal is not at variance with the ideals set for maintaining biodiversity in the region. It seems rather that most of the species identified as occurring typically on post-mined regeneration sites may in fact contribute to the local abundances of these species found in the region.

Chapter 6

Synthesis

The rehabilitation of mined sites north of Richards Bay along the coast of KwaZulu-Natal (South Africa) resulted in a known age successional sere ranging in age from 1 to 21 years at the time of the present study. The unmined area of the region consists of patches of mature coastal dune forest, patches of artificially maintained grasslands, and woodlands in various stages of regeneration and patches of poorly maintained exotic timber plantations. All these patches are inhabited by a range of indigenous bird species and as a consequence provided an opportunity to address the objectives as outlined before.

The first part of my thesis examines the assumption of Kritzinger & van Aarde (1998) that the bird assemblages of different known age successional seral stages of coastal dune development follow similar developmental pathways. Based on two bouts of instantaneous sampling five years apart the structural bird community variables (species diversity, total density and evenness) increase with regeneration age and on both occasions converged in similarity towards the variables recorded on the “bench-mark” mature forests. However, during the second study bout total density did not increase with habitat regeneration as recorded by Kritzinger & van Aarde (1998) for the first study bout. Changes in species compositions resulted from an increase in the rate of species addition as succession progress, while species replacement tend to decrease. Therefore, as the habitat changes through the progress of succession so do the species composition changes, with different species typical for each seral stage. As expected the species typical of these later developmental stages were characterised by K – selected traits, while those of early successional stages of vegetation development were characterised by r-selected traits.

It seems that habitat selection in the course of succession is probably the main process responsible for the observed patterns. This means that increased habitat structure and heterogeneity (as observed at increased regeneration age) might be correlated to bird

species diversity and bird specialisation (such as foraging habitats and food sources). Density on the other hand fluctuated (bimodal) with regeneration age and are probably not correlated with habitat structure or heterogeneity but rather to seasonal events. This phenomenon gives rise to unpredictable changes (temperature, precipitation) in bird density through time that brought about the differences observed in species compositions between the two study periods. Apart from the above, it seems that the different stages of development differ from each other in species compositions and community structure as well as during different time periods (seasons) and therefore seems that ecological succession is the driving force in bird communities from simple communities to complex communities.

In the second part of the study (Chapter 4) I investigated the possibility that trends in species richness and species diversity within the region can be explained by the intermediate disturbance hypothesis as predicted by Horn (1975), Miller (1982) and Petraitis *et al.* (1989). Three levels of relative disturbances identified both locally and regionally I could not find any evidence in support of the intermediate disturbance hypothesis. The bird communities follow a general monotonic trend with heist diversity and evenness at areas with minimal disturbances. The regional and local trend in community variables appears to be determined by habitat heterogeneity, rather than the level of habitat disturbances or integrity. Also, the hypothesis has only been true for sessile and planktonic organisms, and birds being mobile organisms might therefore reject the hypothesis.

My analyses to determine the contribution of the bird assemblage of the rehabilitating dunes to regional bird community characteristics were based on comparisons of derived structural and compositional variables based on the inclusion and exclusion of data from rehabilitating sites. Implementation of rehabilitation programmes has always raised questions to whether restored systems are at variance with the natural systems in the region. I have found that rehabilitation of bird communities on previously mined coastal dunes does not have any marked effect on bird communities typical to the region. Rehabilitation did create a bird assemblage not typical of the region but this assemblage presence is purely temporal. Therefore, in view of rehabilitation programmes, I can state that bird communities on regenerating coastal dunes of Richards

Bay, northern KwaZulu-Natal (South Africa) are typical of the region and that the rehabilitation process are not facilitating habitats atypical of the surrounding region that may affect the regional bird communities negatively.

Summary

The coastal dunes north of Richards Bay (28°38'S 32°20'E) have been mined by the mining company RBM (Richards Bay Minerals) for heavy metals such as zircon, rutile and ilmenite (Van Aarde *et al.* 1996a). The regeneration of mined dunes through a rehabilitation programme directed at establishing indigenous dune forests resulted in the development of patches of dune vegetation of known age, collectively representing a successional sere of indigenous dune vegetation. Apart from the mining process itself, other disturbance factors (e.g. burning, grazing, clearcutting and logging) in the region have resulted in a series of patches of vegetation ranging from relatively undisturbed dune forests to unmined regenerating dune vegetation and grasslands. Some areas have been severely disturbed through clearcutting and comprise of almost no understorey, while other patches consist of a mixture of poorly maintained exotic timber species. Each of these patches of vegetation support bird assemblages, some of which may be atypical for the region. Some of these assemblages may comprise of species endemic to the region or may occur at relatively low numbers as a consequence of these man-induced habitat disturbances.

The development of the bird community of regenerating dune forests in my study area was associated with changes from species typical of grasslands to species typical of woodlands. Based on an earlier study (Kritzinger & van Aarde 1998), trends in species richness, species diversity and species composition along an age gradient of spatially separated sites, the development of these bird communities are similar to those recorded elsewhere along successional gradients. The present study compares age related changes in species composition, species richness and species diversity of the bird community during instantaneous sampling five years after the 1993/94 study of Kritzinger & van Aarde (1998) and is based on information collected during 1998/99. It also addresses the intermediate disturbance hypothesis as an explanation for trends in community variables noted for the region and investigates the contribution of rehabilitating habitats to regional diversity.

Line transects surveys were conducted on 16 sites in the study area, these representing a disturbance regime from relatively undisturbed forests to severely disturbed plantations dominated by poorly maintained exotic timber species. The sites regenerating in response to dune rehabilitation represented an area of intermediate disturbance. Surveys were done along fixed line transects and the number of lines surveyed in a given site depended on the area of the site. Transects were at least 200 meters apart to improve the independence of observations. Furthermore, the starting points of the lines at a particular site were randomised and surveyed for about four hours from half an hour to one hour after sunrise when the birds are most active and conspicuous. Surveys were conducted on a monthly basis from June 1998 to February 1999.

Data from each line transect were analysed using the computer program DISTANCE (Laake *et al.* 1993) to obtain estimates of total bird density ha^{-1} for each sampled site. The relative densities for each species on each sampling site were obtained by using the equation $rD = rN/rV$, where rD is the relative density, rN is the relative number seen (the number of a specific species seen relative to the total number seen on the transect) and rV is relative visibility (Buckland *et al.* 1992). Bray-Curtis similarities of fourth-root transformed species relative densities were calculated between every pair of sampled sites (Clarke & Warwick 1994).

The species richness, total density ha^{-1} , Shannon diversity index and Pielou's evenness index were calculated for each of the sites as the mean values of the transect lines. Rank-abundance and rarefaction curves were constructed for each sampled site as described by Tokeshi (1993) and by James & Wamer (1982) respectively.

The community composition was analysed through multivariate analyses. Non-metric multidimensional scaling (ordination) was used to map inter-relationships between the sampling sites in order to differentiate between bird assemblages. Also, the typical species on each sampled site and discriminant species among the sampled sites were analysed according to Clarke & Warwick (1994).

Species richness, diversity and evenness increased with regeneration age for both study years (1998/99 and 1993/94). The absolute values of bird community variables increased with site regeneration age and values for the post-mined regenerating coastal

vegetation converge in similarity towards those of an unmined relatively mature dune forest. Differences in the derived community structure for the two study periods were small.

Ordination techniques showed that regenerating grassland sites and the intermediately aged regenerating sites form distinct assemblages, while the assemblages on the rest of the regenerating sites were more similar to each other and to those of the mature forest sites. Although the trends recorded through the measured multivariate techniques for the different study periods were the same, differences in the densities of species resulted from seasonal effects.

Species compositions also changed from species typical of grasslands (pioneers) with r-selective traits towards more specialist species (frugivores and non-passerines) with K-selective traits on the older woodland regenerating sites as predicted by successional theory (Pacala & Rees 1998). These species were illustrated by the typical and discriminant species recorded from each site.

The second part of the study examines the intermediate disturbance hypothesis as a factor forcing regional trends in habitat specific species diversity, density and evenness. Community variables increased monotonically with a decrease in the extent of disturbance. Only total density showed peaked values at the intermediate stage of local vegetation regeneration within the intermediately disturbed area. The intermediately disturbed habitats produced the highest number of rare species, while the lowest numbers were recorded from severely disturbed areas. Typical species also declined monotonically from undisturbed areas to severely disturbed areas. The occurrence of rare species was also affected by the state of disturbance within an intermediately disturbed area. The study does not support the intermediate disturbance hypothesis as an explanation for local and regional trends in the macro-parameters of bird assemblages in the study area. Regional trends may result from structural heterogeneity in habitat variables

The third part of the study examines the contribution of the bird assemblages on the post-mined regenerating dunes towards regional diversity. Data for this part of the study were obtained from post-mined regenerating sites, mature forests (Mapelane and

Zulti/Sokhulu), afforested areas (pine, gum and beefwood plantations), unmined sites of coastal dune indigenous woodlands (three sites) and the Cape Vidal/St. Lucia grasslands.

Four distinct assemblages (an assemblage occupying indigenous vegetation, one on exotic timber plantations and two different assemblages on grasslands) were identified when information for all the sites were combined. The exclusion of data from rehabilitated regenerating sites reduced the number of assemblages to three as one grassland assemblage (1-4 years old) disappeared. The exclusion of data from the rehabilitating sites had no influence on structural and compositional values for the region. Therefore, the rehabilitated regenerating area does not harbour bird assemblages atypical for the region and also do not contribute to the presence of rare or endemic species. Dune rehabilitation thus does not create habitats atypical of the region.

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Appendix 1 List of all bird species recorded from the total sampling area for both study periods during both seasons.

FAMILY	COMMON NAME	SCIENTIFIC NAME	AUTHOR
THRESKIORNITHIDAE	Hadeda Ibis	<i>Bostrychia hagedash</i>	Latham
ACCIPITRIDAE	Cuckoo Hawk	<i>Aviceda cuculoides</i>	Swainson
	Longcrested Eagle	<i>Lophaetus occipitalis</i>	Daudin
	Southern Banded Snake Eagle	<i>Circaetus fasciolatus</i>	Gurney
	African Fish Eagle	<i>Haliaeetus vocifer</i>	Daudin
	Steppe Buzzard	<i>Buteo buteo</i>	L.
	Crowned Eagle	<i>Stephanoaetus coronatus</i>	L.
	African Goshawk	<i>Accipiter tachiro</i>	Daudin
	African Marsh Harrier	<i>Circus ranivorus</i>	Daudin
	Gymnogene	<i>Polyboroides typus</i>	Smith
COLUMBIDAE	Redeyed Dove	<i>Streptopelia semitoquata</i>	Rüppell
	Tambourine Dove	<i>Turtur tympanistris</i>	Temminck
	Cinnamon Dove	<i>Aplopelia larvata</i>	Temminck
	Green Pigeon	<i>Treron calva</i>	Wagler
MUSOPHAGIDAE	Livingstone's Lourie	<i>Tauraco livingstonii</i>	Gray
	Purplecrested Lourie	<i>Tauraco porphyreolophus</i>	Vigors
CUCULIDAE	Emerald Cuckoo	<i>Chrysococcyx cupreus</i>	Shaw
	Klaas's Cuckoo	<i>Chrysococcyx klaas</i>	Stephens
	Diederik Cuckoo	<i>Chrysococcyx caprius</i>	Boddaert
	Green Coucal	<i>Ceuthmochares aereus</i>	Vieillot
	Burchell's Coucal	<i>Certhopus burchellii</i>	Swainson
TYTONIDAE	Barn Owl	<i>Tyto alba</i>	Scopoli
STRIGIDAE	Marsh Owl	<i>Asio capensis</i>	A. Smith
CAPRIMULGIDAE	European Nightjar	<i>Caprimulgus europaeus</i>	L.
COLIIDAE	Redfaced Mousebird	<i>Urocolius indicus</i>	Latham
	Spectacled Mousebird	<i>Colius striatus</i>	Gmelin
TROGONIDAE	Narina Trogon	<i>Apaloderma narina</i>	Stephens
HALCYONIDAE	Pygmy Kingfisher	<i>Ispidina picta</i>	Boddaert
	Brownhooded Kingfisher	<i>Halcyon albiventris</i>	Scopoli
MEROPIDAE	Little Bee-eater	<i>Merops pusillus</i>	Müller
BUCEROTIDAE	Trumpeter Hornbill	<i>Bycanistes bucinator</i>	Temminck
	Crowned Hornbill	<i>Tockus alboterminatus</i>	Büttikafer
CAPITONIDAE	Blackcollared Barbet	<i>Lybius torquatus</i>	Dumont
	White-eared Barbet	<i>Stactolaema leucotis</i>	Sundevall
	Redfronted Tinker Barbet	<i>Pogoniulus pusillus</i>	Dumont
	Goldenrumped Tinker Barbet	<i>Pogoniulus bilineatus</i>	Sundevall
INDICATORIDAE	Scalythroated Honeyguide	<i>Indicator variegatus</i>	Lesson
PICIDAE	Goldentailed Woodpecker	<i>Campethera abingoni</i>	A. Smith

(Appendix I continue)

	Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	Vieillot
ALAUDIDAE	Rufousnaped Lark	<i>Mirafra africana</i>	Smith
HIRONDINIDAE	Black Sawwing Swallow	<i>Psalidoprocne holomélas</i>	Rüppell
	Lesser Striped Swallow	<i>Hirundo abyssinica</i>	Guérin-Méneville
CAMPEHAGIDAE	Black Cuckooshrike	<i>Campehaga flava</i>	Vieillot
	Grey Cuckooshrike	<i>Coracina caesia</i>	Lichtenstein
DICRURIDAE	Forktailed Drongo	<i>Dicrurus adsimilis</i>	Beckstein
	Squaretailed Drongo	<i>Dicrurus ludwigii</i>	A. Smith
ORIOOLIDAE	Blackheaded Oriole	<i>Oriolus larvatus</i>	Lichtenstein
CORVIDAE	Pied Crow	<i>Corvus albus</i>	Müller
PYCNONOTIDAE	Blackeyed Bulbul	<i>Pycnonotus barbatus</i>	Desfontaines
	Terrestrial Bulbul	<i>Phyllastrephus terrestris</i>	Swainson
	Sombre Bulbul	<i>Andropadus importunus</i>	Vieillot
	Yellowbellied Bulbul	<i>Chlorocichla flaviventris</i>	Smith
	Yellowspotted Nicator	<i>Nicator gularis</i>	Hartlaub & Finsch
TURDIDAE	Kurrichane Thrush	<i>Turdus libonyana</i>	Smith
	Spotted Ground Thrush	<i>Zoothera guttata</i>	Vigors
	Stonechat	<i>Saxicola torquata</i>	L.
	Natal Robin	<i>Gossypha natalensis</i>	A. Smith
	Cape Robin	<i>Cossypha caffra</i>	L.
	Starred Robin	<i>Pogonocichla stellata</i>	Vieillot
	Cape Rock Thrush	<i>Montocola rupestris</i>	Vieillot
	Bearded Robin	<i>Erythropygia quadrivirgata</i>	Reichenow
	Whitebrowed Robin	<i>Erythropygia leucophrys</i>	Vieillot
SYLVIIDAE	European March Warbler	<i>Acrocephalus palustris</i>	Bechstein
	Willow Warbler	<i>Phylloscopus trochilus</i>	L.
	Garden Warbler	<i>Sylvia borin</i>	Boddaert
	Yellowbreasted Apalis	<i>Apalis flavida</i>	Strickland
	Rudd's Apalis	<i>Apalis ruddi</i>	Grant
	Longbilled Crombec	<i>Sylvietta rufescens</i>	Vieillot
	Bleating Warbler	<i>Camaroptera brachyura</i>	Vieillot
	Fantailed Cisticola	<i>Cisticola juncidis</i>	Rafinesque
	Palecrowned Cisticola	<i>Cisticola brunnescens</i>	Heuglin
	Croaking Cisticola	<i>Cisticola natalensis</i>	A. Smith
	Rattling Cisticola	<i>Cisticola cheniana</i>	A. Smith
	Tawnyflanked Prinia	<i>Prinia subflava</i>	Gmelin
MUSCICAPIDAE	Dusky Flycatcher	<i>Muscicapa adusta</i>	Boie
	Spotted Flycatcher	<i>Muscicapa striata</i>	Pallas
	Bluegrey Flycatcher	<i>Muscicapa caerulescens</i>	Hartlaub
	Black Flycatcher	<i>Melaenornis pammelaina</i>	Stanley
	Pallid Flycatcher	<i>Melaenornis pallidus</i>	Müller
	Woodwards' Batis	<i>Batis fratrum</i>	Shelley
	Wattle-eyed Flycatcher	<i>Platysteira peltata</i>	Sundevall

(Appendix I continue)

	Bluemantled Flycatcher	<i>Trochocercus cyanomelas</i>	Vieillot
	Paradise Flycatcher	<i>Terpsiphone viridis</i>	Müller
MOTACILLIDAE	Grassveld Pipit	<i>Anthus cinnamomeus</i>	Rüppell
	Cape Wagtail	<i>Motacilla capensis</i>	L.
	Pied Wagtail	<i>Motacilla aguimp</i>	Dumont
	Yellowthroated Longclaw	<i>Macronyx croceus</i>	Vieillot
LANIIDAE	Fiscal Shrike	<i>Lanius collaris</i>	L.
	Lesser Grey Shrike	<i>Lanius minor</i>	Gmelin
MALACONOTIDAE	Southern Boubou	<i>Laniarius ferrugineus</i>	Gmelin
	Puffback	<i>Dryoscopus cubla</i>	Shaw
	Gorgeous Bush Shrike	<i>Telephorus quadricolor</i>	Cassin
	Orangebreasted Bush Shrike	<i>Telephorus sulfureopectus</i>	Lesson
	Blackcrowned Tchagra	<i>Tchagra senegala</i>	L.
STURNIDAE	Blackbellied Starling	<i>Lamprotornis corruscus</i>	Nordmann
NECTARINIIDAE	Purplebanded Sunbird	<i>Nectarinia bifasciata</i>	Shaw
	Grey Sunbird	<i>Nectarinia veroxii</i>	A. Smith
	Scarletched Sunbird	<i>Nectarinia senegalensis</i>	L.
	Olive Sunbird	<i>Nectarinia olivacea</i>	A. Smith
	Collared Sunbird	<i>Anthreptes collaris</i>	Vieillot
ZOSTEROPIDAE	Cape White-eye	<i>Zosterops capensis</i>	Swainson
PLOCEIDAE	Thickbilled Weaver	<i>Amblyospiza albifrons</i>	Vigors
	Forest Weaver	<i>Ploceus bicolor</i>	Vieillot
	Spectacled Weaver	<i>Ploceus ocularis</i>	A. Smith
	Lesser Masked Weaver	<i>Ploceus intermedius</i>	Rüppell
	Yellow Weaver	<i>Ploceus subaureus</i>	A. Smith
	Weavers	<i>Ploceus spp.</i>	-
	Redshouldered Widow	<i>Euplectes axillaris</i>	A. Smith
ESTRILDIDAE	Green Twinspot	<i>Mandingoa nitidula</i>	Hartlaub
	Bluebilled Firefinch	<i>Lagonostica rubricata</i>	Lichtenstein
	Blue Waxbill	<i>Uraeginthus angolensis</i>	L.
	Common Waxbill	<i>Estrilda astrild</i>	L.
	Grey Waxbill	<i>Estrilda perreini</i>	Vieillot
	Bronze Mannikin	<i>Spermestes cucullatus</i>	Swainson
	Redbacked Mannikin	<i>Spermestes bicolor</i>	Fraser
VIDUIDAE	Pintailed Whydah	<i>Vidua macroura</i>	Pallas
FRINGILLIDAE	Yelloweyed Canary	<i>Serinus mozambicus</i>	Müller
	Cape Canary	<i>Serinus canicollis</i>	Swainson
	Bully Canary	<i>Serinus sulphuratus</i>	L.

Appendix 2 The rare species recorded from each level of disturbance (✓) and each level of disturbance within the intermediately disturbed area (✓✓).

Species	Relatively undisturbed	Intermediately disturbed	Severely disturbed
Barn Owl	✓		
Blackbellied Starling	✓		
Blackcrowned Tchagra			✓
Blackeyed Bulbul		✓	
Bluemantled Flycatcher	✓		
Brownhooded Kingfisher		✓	✓
Bully Canary			✓
Burchell's Coucal		✓	✓
Cape White-eye		✓	
Cardinal Woodpecker		✓	
Collared Sunbird			✓
Crowned Hornbill	✓		
Cuckoo Hawk		✓	
Dusky Flycatcher		✓	
Emerald Cuckoo		✓	
European Nightjar	✓		
Fiscal Shrike		✓	
Forest Weaver		✓	
Gorgeous Bush Shrike		✓	
Goldenrumped Tinker Barbet		✓	✓
Green Coucal	✓	✓	
Green Pigeon	✓		
Greenspotted Dove			✓
Grey Sunbird			✓
Hadedda Ibis	✓		
Klaas's Cuckoo	✓		
Lesser Masked Weaver	✓	✓	
Lesser Striped Swallow			✓
Livingstone's Lourie			✓
Longbilled Crombec		✓	
Longcrested Eagle	✓		
Narina Trogon		✓	
Natal Robin		✓	
Puffback		✓	
Purplebanded Sunbird		✓	
Purplecrested Lourie	✓		✓
Pygmy Kingfisher			✓
Rattling Cisticola		✓	
Redeyed Dove		✓	✓
Rudd's Apalis	✓		
Sombre Bulbul		✓	
Southern Boubou		✓	
Spectacled Weaver			✓
Squaretailed Drongo		✓	
Tambourine Dove		✓	✓
Tawnyflanked Prinia		✓	
Thickbilled Weaver	✓		
Trumpeter Hornbill	✓		

(Appendix 2 continue)

Whitebrowed Robin	<i>Erythropygia leucophrys</i>		✓	
Yellowbellied Bulbui	<i>Chlorocichla flaviventris</i>			✓
Yelloweyed Canary	<i>Serinus mozambicus</i>		✓	
Yellowspotted Nicator	<i>Nicator gularis</i>	✓	✓	

Species		Least disturbed	Intermediately disturbed	Severely disturbed
Blackeyed Bulbul	<i>Pycnonotus barbatus</i>	✓✓	✓✓	
Brownhooded Kingfisher	<i>Halcyon albiventris</i>	✓✓		
Burchell's Coucal	<i>Cenrtopus burchellii</i>		✓✓	
Cape Canary	<i>Serinus canicollis</i>			✓✓
Cape White-eye	<i>Zosterops capensis</i>	✓✓	✓✓	
Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	✓✓		
Collared Sunbird	<i>Anthreptes collaris</i>		✓✓	
Common Waxbill	<i>Estrilda astrild</i>			✓✓
Cuckoo Hawk	<i>Aviceda cuculoides</i>	✓✓		
Dusky Flycatcher	<i>Muscicapa adusta</i>	✓✓		
Emerald Cuckoo	<i>Chrysococcyx cupreus</i>	✓✓		
Fiscal Shrike	<i>Lanius collaris</i>		✓✓	✓✓
Forest Weaver	<i>Ploceus bicolor</i>		✓✓	
Georgeous Bush Shrike	<i>Telephorus quadricolor</i>		✓✓	
Goldenrumped Tinker Barbet	<i>Pogoniulus bilineatus</i>		✓✓	
Green Coucal	<i>Ceuthmochares aereus</i>		✓✓	
Lesser Masked Weaver	<i>Ploceus intermedius</i>		✓✓	
Little Bee-eater	<i>Merops pusillus</i>			✓✓
Longbilled Crombec	<i>Sylvietta rufescens</i>	✓✓	✓✓	
Narina Trogon	<i>Apaloderma narina</i>		✓✓	
Natal Robin	<i>Gossypha natalensis</i>		✓✓	
Palecrowned Cisticola	<i>Cisticola brunnescens</i>			✓✓
Pintailed Whydah	<i>Vidua macroura</i>			✓✓
Puffback	<i>Dryoscopus cubla</i>		✓✓	
Purplebanded Sunbird	<i>Nectarinia bifasciata</i>	✓✓		
Rattling Cisticola	<i>Cisticola cheniana</i>	✓✓		
Redeyed Dove	<i>Streptopelia semitoquata</i>		✓✓	
Scarletched Sunbird	<i>Nectarinia senegalensis</i>			✓✓
Sombre Bulbul	<i>Andropadus importunes</i>		✓✓	
Southern Boubou	<i>Laniarius ferrugineus</i>	✓✓	✓✓	
Squaretailed Drongo	<i>Dicrurus ludwigii</i>		✓✓	
Tambourine Dove	<i>Turtur tympanistria</i>	✓✓		
Tawnyflanked Prinia	<i>Prinia subflava</i>	✓✓		
Whitebrowed Robin	<i>Erythropygia leucophrys</i>	✓✓		
Yelloweyed Canary	<i>Serinus mozambicus</i>		✓✓	✓✓
Yellowspotted Nicator	<i>Nicator gularis</i>		✓✓	