

20. Continental Diversity Patterns and Convergent Evolution in Bird Communities

M. L. CODY

20.1 Introduction

Convergent evolution in mediterranean-climate ecosystems has received intensive study over the last decade. At this stage, with considerable data on bird community structure available from all five continents on which mediterranean-type habitats exist, there are both similarities and dissimilarities to be interpreted and resolved. In this paper I compare patterns of alpha and beta diversity in bird communities of California, Chile, Sardinia and South Africa and point out what questions remain unanswered, how they can be refined, and what sorts of data might help to answer them. I then discuss data from South Africa which help illuminate some of the factors that control species diversity patterns within continents, especially at the levels of β and γ diversity.

The chapter uses the review of convergent evolution and α diversity by Cody and Mooney (1978) as a point of departure, then compares β diversity over matched habitat gradients, emphasizing broad differences between continents and among transects within a single region of South Africa. Birds on similar habitat gradients in three different areas of Cape Province show reasonable similarities in α diversity, but strikingly different β diversity patterns. I attribute the similarities to the matched vegetation in the three gradients, and the dissimilarities to differences both in total habitat area available to the birds and in the distribution of this habitat area over the gradient from low, open vegetation to taller and denser fynbos and woodland.

Our understanding of continental diversity patterns is still rather rudimentary. It will develop, I believe, by use of concise and quantitative definitions of different components of this diversity, and a realization that the controlling factors for each component may be quite independent. I discuss these conceptual questions, point out what I see as the major unknowns for each component of this diversity, and sketch the ways in which these components interact. In the final section of the paper I get back to the real world of ecological biogeography with presentation and discussion of data recently collected on South Africa. I ask whether the clear-cut examples of habitat patchiness within a continental setting,

such as the string of patches of Afromontane woodland that stretch westward from Knysna, can be extrapolated to a more subtle effect on diversity within complex mosaics of variable habitat. A detailed analysis of bird distributions over habitats in the three areas of Cape Province mentioned above illustrates this theme. The geographic position of each site censused, relative to the distributions of its habitat type over the map - karoo, fynbos, forest etc. - affects the α diversity of birds within the habitat type, bird species turnover (β diversity) between habitat types, and turnover within habitat types between each of the three geographic areas (γ diversity).

20.2 Convergent evolution at the community level

20.2.1 MACCHIA SITES OF FOUR CONTINENTS

A detailed analysis of convergent and nonconvergent evolution in birds and plants of matched sites on four continents has been published earlier (Cody and Mooney 1978). The sites compared are from the chaparral of southern California, the matorral of central Chile, macchia in southern Sardinia and fynbos in South Africa. All sites enjoy the characteristic mediterranean temperature and precipitation regime, but there are climatic differences among sites that appear to be reflected in both the plant and bird ecologies. In addition, two control sites were used, one in Yorkshire with similar vegetation structure (successional thorn scrub) but a different climate, a second in California, evergreen oak woodland with a different vegetation structure but similar (mediterranean) climate. For details of site locations, vegetation and bird census methods, see Cody and Mooney (1978) and references therein.

The four "experimental" sites all support a thick and fairly continuous scrub cover 2-3 m high, with both broad- and narrow-sclerophyllous plants, and all four appear very similar. Both plants and birds differ taxonomically among sites; the sites share on the average 48% of their bird families, 10% of their genera and only 2% of their bird species. On 2.5-4-ha sites with homogeneous vegetation, total bird species seen in the breeding season were 24 in Sardinia, 28 in South Africa, 30 in California and 31 in Chile. The eight most abundant species at each site comprised 74% of the total bird density at Sardinia, 70% in South Africa, 79% in California and 67% in Chile, while total bird densities were assessed at 13.3, 9.3, 14.4 and 16.6 pairs ha^{-1} respectively.

At each site the birds were assembled into rough guilds according to foraging ecology. Each site had at least four species of foliage insectivores, at least six species of ground-foraging omnivores, two to four species of seed and fruit eaters, one aerial feeder, one crepuscular insectivore ("nightjar-type") and two to four of raptors and scavengers. Each site except Sardinia (with none) had one to two woodpeckers, each site except Sardinia (with a single medium-sized species) had a small and a larger flycatching species, and each site except Sardinia (with none), two to three nectarivorous species. The insular position of Sardinia may account for the absence of the first-mentioned rather more specialized species, but not for the lack of nectarivores.

Despite some overall similarity in guild structure among the four sites, differences do appear. For example, Chile has only four species (5.8 pairs ha^{-1}) of foliage insectivores whereas Sardinia has nine species (7.7 pairs ha^{-1}) compared to the average 6.2 species (5.6 pairs ha^{-1}). But Chile has 12 species of ground omnivores totalling 7.1 pairs ha^{-1} versus

the average 8.3 species with 4.8 pairs ha⁻¹. And whereas Chile and California have two species each with 1.1 and 1.2 pairs ha⁻¹ respectively of nectarivores, the three South African species total 2.7 pairs ha⁻¹.

We used the two control sites to calibrate these purportive similarities and differences in species numbers and densities. Both species numbers (36) and total bird densities (20.7 pairs ha⁻¹) were higher in California oak woodland. In particular, the species numbers and densities in the categories of foliage insectivores, sallying flycatchers and seed and fruit eaters are two to three times that of the average macchia site. In the Yorkshire successional scrub species numbers (31) and densities (18.6 pairs ha⁻¹) resemble those of macchia, but the distribution of species numbers and densities among guilds is different. The ground-foraging omnivores comprise the largest category with 12 species and 7.9 pairs ha⁻¹; in addition foliage insectivores are more numerous (10 versus average 6.2 species), flycatchers are rarer (0.1 versus average 0.7 pairs ha⁻¹) and seed and fruit eaters much commoner than in macchia (5 species, 4.1 pairs ha⁻¹ versus an average 3 species, 0.9 pairs ha⁻¹).

20.2.2 DENSITY COMPENSATION

Community organization may be more similar than the differences in species numbers among the different macchia communities indicate. Through density compensation, fewer species can make up, at least in part, for the absence of ecologically similar competitors, and by foraging over a broader height interval or in a wider variety of ways support more pairs ha⁻¹ in species-poor sites. Thus the fewer Chilean foliage insectivores are denser (1.44 pairs ha⁻¹ species⁻¹) than the overall average for the four sites (0.90 pairs ha⁻¹/species⁻¹), and the larger number of ground foragers in Chile are each less dense (0.59 pairs ha⁻¹ species⁻¹) than the average in Sardinia and California (0.73 and 0.76 pairs ha⁻¹ species⁻¹ respectively). Yet there are instances where no density compensation is apparent: the three species of nectarivores in South African fynbos are each more common than the two nectarivores in California and Chile (0.89 versus 0.57 pairs ha⁻¹ species⁻¹). And finally, there are major discrepancies in the total bird densities among sites, greatest between the South African and Chilean sites (80%), and in general much greater than the differences between species totals (up to 30%).

20.2.3 DIFFERENCES IN FOOD RESOURCES

Similarities in community organization (guild structure, species numbers and relative abundances) may follow from broad similarities in climate and vegetation structure among the different sites, whereas differences in bird densities may reflect differences in food resources. The only resource that I have directly measured is that which bears directly on flycatcher and foliage insectivore densities, the insect catches on Tanglefoot plaques. These catches are reasonable estimates of the food available to insectivorous birds, since in Arizona pine-oak woodland (Cody 1981) and in Moroccan macchia (Cody 1980b) 70% and 85% of the variation in bird densities is accounted for by variation in Tanglefoot catches respectively. In the macchia sites, total bird density D is directly related to the area A under the graph of insects caught versus height above ground: $D = 8 + A/25$; South African insect catches were three to four times lower than those in California and Chile, where foliage

insectivores and flycatchers are two and a half times as common. In other aspects also the resources are not well matched among sites. There are no nectar-producing plants north of the Mediterranean that are morphologically adapted to use by birds, and hence no nectarivorous birds in Sardinia. In South Africa, many nectar-producing plants in the families Proteaceae and Ericaceae are coevolutionarily associated with bird consumers. No plants comparable to the Proteaceae exist in Chile or California; their evolution appears tied to nitrogen- and phosphorus-poor soils, and their flowering and leafing strategies result in more nectar and fewer insects (on the relatively well-defended leaves).

The other major anomaly of high diversity and abundance of ground foragers in Chile is attributable to the matorral having a more open canopy and more summer rainfall. Therefore spring and summer annual plants are important components of that vegetation, and this presumably results in more and various bird food near and on the ground.

20.2.4 COMMUNITY COMPARISONS IN PHENOTYPES AND FORAGING ECOLOGY

Factor analysis of bird phenotype was used to explore questions about the range of morphotypes and of feeding ecologies, and the interrelations among the two sets of observations by cross-continent comparisons. The following conclusions were reached.

- (a) The same range of phenotypes is present in macchia on each continent. The principal components of the seven morphological characters used are similarly constituted on each continent, and species morphotypes from each continent are distributed with statistically indistinguishable means and variances on the morphological plane of the first two principal components.
- (b) Foraging behaviours are similar among the four communities. The first two principal components of foraging behaviour are similarly constituted on each continent, account for similar amounts of behavioural variation (89 ± 4%), and there are no significant differences among continents in the means and variances of species in this behavioural plane.
- (c) The components of foraging ecology covary similarly on the four continents. The principal components of foraging behaviour and foraging height show that (i) faster species forage higher and (ii) species with long pauses in foraging sequence are more variable in foraging height. Species from each continent show statistically similar ranges and means on these two variables, but the South African species exploit a narrower range in relation (ii) above. Canonical correlation between morphology and feeding height first segregates long-winged and short-tailed birds with high foraging ranges from larger, longer-legged and -tailed species that forage on the ground. This relation is not significantly different among continents, despite the fact that in the South African community the composition of the canonical variables is somewhat different. A similar analysis of morphology versus foraging behaviour shows that there are no differences among continents in the way these variables are related. In general, a given foraging behaviour is conducted at a given height in a certain vegetation density similarly on all continents, and phenotypes vary with foraging behaviour in the same way on all continents.

20.3 Bird turnover rates along habitat gradients

20.3.1 ALPHA AND BETA DIVERSITY ON MEDITERRANEAN HABITAT GRADIENTS

Whereas α diversity measures the number of species that pack into and coexist in a given habitat type, a second and potentially independent diversity component is β diversity, the rate at which these species are replaced by others as habitat structure varies. Most habitat variability follows a gradient based on the structure of the vegetation, and thus habitat can be considered a continuous variable H . As H is sampled from low to high values bird species are added to a cumulative list whilst others are lost. The functions $g(H)$ and $l(H)$ describe the way in which species are gained and lost over habitats H respectively. I have defined α diversity as the difference between the species gain and loss functions, $g(H) - l(H)$, itself a function of H , and β diversity as the average rate at which species are gained and lost at a given H : $d/dH(\frac{1}{2}[g(H) + l(H)])$; H is calculated as the logarithm of the principal component of vegetation height and vegetation half-height (Cody 1975).

Bird diversity along similar habitat gradients in the mediterranean-climate zones of California, Chile and South Africa was the subject of an earlier paper (Cody 1975). I have added bird censuses from Sardinia (Appendix A; discussed in Cody 1980a) and two additional transects from South Africa, one in the Outeniqua and Swartberg Mountains in the southern Cape Province and the other from the Cedarberg in the northwestern Cape Province. The three South African transects are the subject of detailed analysis in following sections; here I simply use their α and β diversity curves in a comparative fashion, and give further details of the sites later.

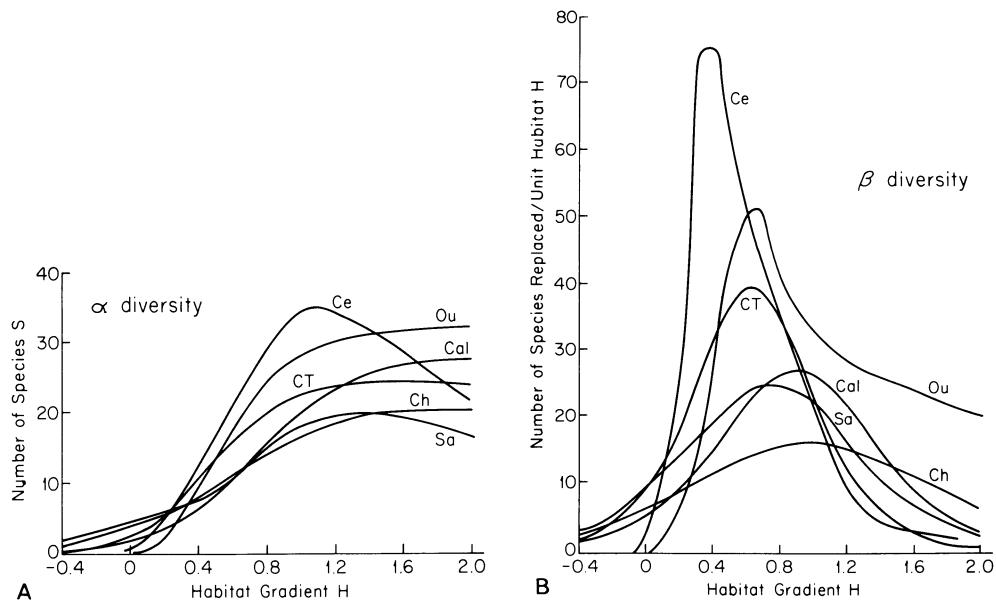


Fig. 1. Plots of α and β diversity over a gradient of mediterranean-climate habitats in six different areas. Four continents are represented. Ch: Chile, Sa: Sardinia, Cal: California, Ce: Cedarberg, Ou: Outeniqua Mountains, CT: Cape Town area, the last three in South Africa. A. α diversity. B. β diversity.

Fig. 1A shows bird α diversity plotted against habitat; fynbos habitats are located at around $0.8 < H < 1.2$, with shorter, more open and drier habitats to the left and taller, mesic woodlands to the right. The number of bird species increases with increasing H in an approximately sigmoid fashion, but in habitats taller than $H = 1$ species numbers increase at a decreasing rate, and may decrease in woodlands. Fig. 1B gives comparable data on β diversity. Unlike curves of α diversity, the species turnover rates on the gradient are quite different between transects. β diversities are highest overall in South Africa, where they peak at lower H values. California and Sardinia are similar with maximum β diversities of 25 species per unit H around $H = 1.0$. Chile has the lowest β diversity, and its maximum of 16 species per unit H is nearly five times lower than figures from the Cedarberg, and three times lower than those in the Outeniqua-Swartberg Mountains. These differences contrast to differences in α diversity among transects that are at most a factor of two and usually much less.

20.3.2 DIVERSITY AND HABITAT AREA

There are two reasonable and empirically acceptable sorts of relationships between α diversity and habitat area. The first is illustrated by the peninsula phenomenon: species diversity in general decreases from the proximal to the distal end of peninsulas. Less obviously, α diversity declines in more isolated or peripheral locations, and in areas isolated by topographic or vegetational discontinuities. The second sort of relationship takes account of the abundance in a region of a particular habitat. Common habitats are in general richer in species (other things being equal) than are rare habitats. Thus it is the rain forests of South America that are rich in bird species, while its savannas are relatively impoverished, but in Africa the reverse is true. These two types of relationship refer to the shape and area of habitat respectively.

The relationships between β diversity and habitat area are more obscure, but some might be extrapolated from the foregoing. For example, if two habitat types adjacent on H are both common, then species are more likely uniquely adapted to each and consequently a high species turnover will occur between the two habitats, even though they are adjacent on the map. If a habitat type occurs as isolated patches, a consequent reduction in α diversity might permit species in habitats adjacent both on H and on the map to move into the patches with a resulting reduction in β diversity. Relations like these are largely speculative, and must be explored.

Table 1 shows for each of six transects, the total "source area" of habitat within 1600 km of the sample sites and its distribution over H . Habitat "shadowed" from the transect locality by mountains in excess of 1500 m is not included as source area. This method is explained in Cody (1975); Acock's (1975) map of veld types is used for South Africa, and a vegetation map by Sahab (1966) gives the information for the mediterranean region. The figures of habitat availability are related to α and β diversity in Fig. 2. In Fig. 2A the diversity data define curves for each transect in the $\alpha - \beta$ plane, with the H values corresponding to the given α and β diversity values shown for each curve. On Fig. 2B habitat isolines join the same habitat points on different transects, and the figures on these isolines show the cumulative habitat area reached by a given H value on the gradient. Thus from Table 1, by $H = 0.6$ on the Californian transect $.39 \times 24.5 = 9.6$ units (10^5 km^2) of habitat area are accumulated, so this value appears on Fig. 2B, second from the left on the third curve up, where

$\alpha = 11$ and $\beta = 24$. Notice that increased habitat availability in general enhances diversity; at low H more habitat influences chiefly β diversity, while more area at higher H promotes greater α diversity.

Table 1. Habitat characteristics around bird census transects in California, South Africa, Chile and Sardinia-Corsica. Total habitat is given in both km^2 (first column) and mi^2 (second column). The area under the $\alpha - \beta$ curve is calculated from Fig. 2A and is in arbitrary units.

Transect	Total Habitat Area (10^5)	Area under $\alpha - \beta$ curve	Cumulative proportion of habitat up to $H =$							
			-0.2	0.2	0.6	1.0	1.4	1.8	2.2	
California	24.5	9.5	160	.03	.21	.39	.58	.66	.81	1.0
Cape Town	22.5	8.7	191	.05	.22	.51	.79	.95	.98	1.0
Cederberg	25.0	9.7	419	.10	.30	.55	.81	.96	.99	1.0
Outeniqua	24.1	9.3	350	.05	.20	.49	.78	.95	.99	1.0
Chile	3.4	1.3	69	.15	.29	.50	.71	.88	.96	1.0
Sardinia	40.2	15.5	94	.07	.39	.68	.77	.81	.87	1.0

Because the lines of Fig. 2B reflect internally consistent effects, rough algorithms can be generated as in Figs 2C and 2D. In Fig. 2C assume that the distribution of habitat over H is uniform, but that larger habitat areas are available, from $5 \times 10^5 \text{ km}^2$ in distribution (i) to $30 \times 10^5 \text{ km}^2$ in distribution (vi). Increasing habitat area produces the set of $\alpha - \beta$ curves shown in the figure. Fig. 2D shows the diversity curves produced by habitat distributions that vary from a preponderance of low habitat (vi) to mostly tall habitat (i), leaving total habitat area constant at $20 \times 10^5 \text{ km}^2$. In each circumstance a different $\alpha - \beta$ curve will result, conforming to the known relationships as they are currently understood.

Figures for habitat availability on the Sardinia-Corsica transect are included on Fig. 2B inside dashed circles. While habitat availability in this region is high, the transects were made on islands and thus a major proportion of this available habitat is isolated from the transect by the Mediterranean Sea. The Sardinia-Corsica data allows us to infer, from their positions relative to continental sites, that these islands have an effective area of available habitat around one-third that measured in my conventional way. Thus we can estimate the efficacy of sea barriers compared to overland barriers.

To return to the data shown in Fig. 2A, my a posteriori explanation for a low α and β diversity over the Chilean transect is that the total habitat area there is small; the Andean cordillera reduces available source habitats to the strip between the mountains and the coast. This restricts immigrant species, reduces α diversity and thus favours habitat generalists and low β diversity. The California and Cape Town transects have a similar area of source habitat, but more of this habitat is woodland and forest in California, where consequently α diversity is higher at higher H . Around Cape Town there is more habitat around $0.6 < H < 1.0$, and this is where Cape

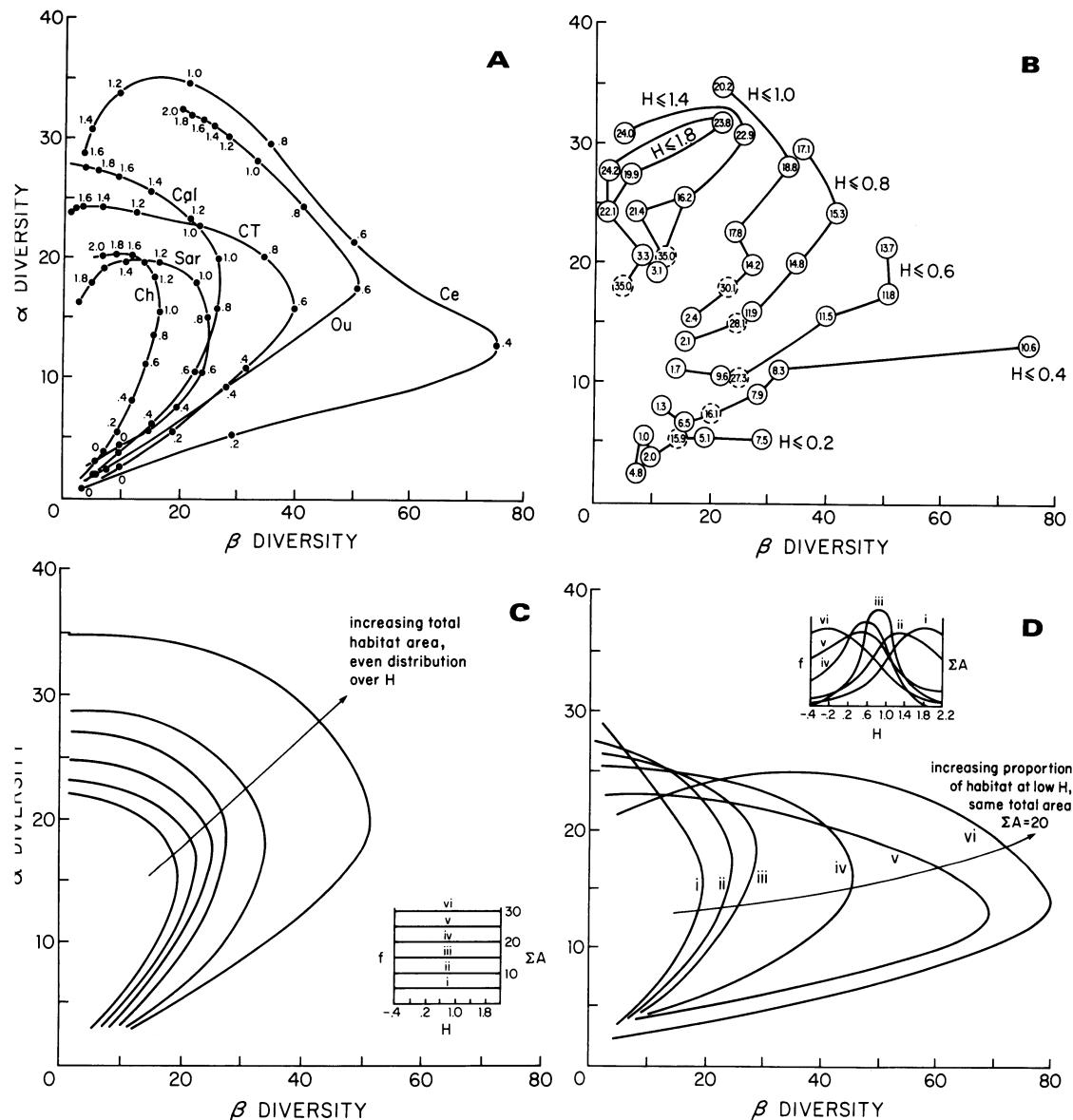


Fig. 2. The α and β diversity data of Fig. 1 are replotted in the diversity plane $\alpha - \beta$. The figures on each curve represent the values of habitat H on the gradient by which the given α and β diversity values are reached (A). In B lines are drawn which connect points at the same H -values in different regions. The encircled figures on these lines are cumulative habitat area (km^2) reached in a given region under curves that describe how much habitat area of each type is available there (see text). If habitat availability is described by a uniform distribution over H , as in the inset graph of C, larger total areas of habitat (i) through (vi) will produce $\alpha - \beta$ curves as shown in C from innermost for smallest total habitat area to outermost for largest total habitat area. In D total habitat area is held constant, while its distribution over habitat type H varies. This produces the $\alpha - \beta$ curves shown. See text for further discussion.

Town β diversity is highest. Comparing the remaining two South African transects to that near Cape Town, both the Outeniqua and the Cedarberg transects have larger source areas (since they are not centred at the tip of the continent) and higher total bird diversities (area under the $\alpha - \beta$ curve of Fig. 2A). The Cedarberg has a variety of habitat with low H values - strandveld, renosterveld and karoid bushveld - each available in the source area over large and topographically simple areas. This gives a maximum β diversity value at $H = 0.4$, and high α diversity values up to $H = 1.0$, but thereafter the lack of habitat with $H > 1.4$ causes α diversity to plunge. In the Outeniqua Mountains transect there is none of the low- H strandveld habitat, only renosterveld and the taller valley bushveld, and thus β diversity peaks at higher H . But this transect is located close to quite large forest areas to the east and north-east, and this influence is seen in a continually rising α diversity and a β diversity that remains high at the largest H values.

20.3.3 CONVERGENT EVOLUTION AND DIVERSITY ON HABITAT GRADIENTS

Both theory and common sense lead us to expect that competition among consumer species for limited resources will place an upper limit on α diversity and will shape the ecologies and morphologies of these consumers by jointly minimizing interspecific overlap and maximizing resource utilization. To the extent that habitats present to consumers similar densities and distributions of resources, we can expect convergent evolution to produce parallel α diversities, consumer densities, and community organization. But to the extent that these habitats differ among continents in their total areas, in the continuity of these areas, and in the accessibility of the habitat to potential colonists from similar habitat nearby, then α diversity might be expected to vary. In particular, in discontinuous or scarce habitats α diversity might equilibrate at levels below those permitted by competition among the members of a large and accessible species pool.

Since α diversity and β diversity are never entirely independent of each other, the factors that produce convergent evolution at the community level are likely to have some influence on β diversities. But this influence appears slight; β diversity is controlled more by topography, habitat continuity and contiguity than by such predictable biological factors as competition and adaptation to habitat-specific challenges of food supply and predators. Thus there is very little reason a priori to expect convergent evolutions in β diversities, and only in such circumstances of parallel distributions of habitat area and habitat availability is such convergence likely to be seen.

20.4 Effects of habitat contiguity

20.4.1 HABITAT PATCHES AS ISLANDS

Real islands are discrete parcels of land surrounded by water, but to express the difficulty of reaching the island as simply proportional to the width of the water barrier is a simplification that ignores the fact that a certain stretch of water might be far more of a barrier to one species than to another (Case and Cody 1982). These problems are magnified where isolation is by different habitats rather than by water gaps. Rosenzweig (1975) talks about "habitat taboos" in his discussion of continental

analogies to island biogeography theory, and Cody (1975) related this notion to β diversity; it is epitomized by the striking fact that exotic habitats go virtually unoccupied by birds in regions where the β diversity in native vegetation is high, but are well populated in regions of low β diversity. Thus in the mediterranean zones of Chile and South Africa, pine and eucalyptus plantations support diverse and dense bird communities in the former, but are virtual deserts in the latter country.

In continental landscapes habitats occur naturally as mosaics, since vegetation structure as well as plant species vary with varying soil type, slope, aspect, fire and management history as well as climate. Thus patches of like habitat are often separated by intervening habitat of a different type that constitutes both a physical barrier, in terms of a stretch of alien terrain, and a biological barrier, since it is likely to contain competitor species that render the habitat additionally inhospitable. Here the black and white of land versus water becomes an intermediate grey, and we can rely on only empirical facts to estimate the importance of habitat barriers to the distribution of birds within continents.

These two aspects of continental distributions, the natural occurrence of a certain habitat type in a patchwork, and the varying degrees to which intervening habitats constitute a barrier to would-be colonists, have received very little attention from biogeographers and ecologists, yet it seems that their understanding is fundamental to both theoretical and analytical studies of distribution. The outcome of adaptation and competition among species that inhabit a patchwork environment is basically different from that in broad continuous habitat (Levins and Culver 1971; Horn and MacArthur 1972), and the same is true for habitats that are patchy in time (Levins 1968). Thus where habitats are patchy and/or rare there may be an increasingly important role for species with good invasion but poor competitive capacities which prevent the evolution of equilibrial communities. Such species would increase α diversity and decrease β diversity in patchy, marginal or rare habitat, and might through temporary overexploitation of resources be found in unexpectedly high densities (Diamond 1974; Case et al. 1979). This and other real-island phenomena are likely to show up in modified form on continents with habitat mosaics, but both the concepts and the data base are poorly developed. We know that North American mammals of pine and fir woodlands have not crossed desert barriers of modest width in thousands of years (Brown 1971), that many forest birds on the New Guinea coast will not cross water gaps of a few metres whereas others routinely fly thousands of miles to reach new islands (Diamond 1975), that isolated granitic buttes serve as habitat islands to saxicolous plants (Cody 1978) and so do thistleheads for phytophagous insects (Brown and Kodric-Brown 1977), but facts such as these have yet to be organized into a theory of continental diversity to parallel that developed for real islands.

20.4.2 THE AFROMONTANE WOODLAND PATCHES IN CAPE PROVINCE

When habitats of a distinct type occur in very small and very isolated patches, then the effects of these island-like characteristics on the resultant communities are readily observed; the Afromontane forest of the southwestern part of Cape Province is a good example. This distinctive 20-30 m evergreen vegetation is fairly continuous east of Knysna (White 1978), but between George and Cape Town exists in patches that become smaller and more isolated from the main forest block as one moves west. A

detailed analysis of the plant communities in these forest patches is given by MacKenzie (1978), and of the bird communities by Cody (1982); here I will refer only to some of the most obvious results of habitat patchiness.

The distribution of the largest patches of Afromontane forest between George and Cape Town is shown in Fig. 3. Censuses of the birds were made at five sites: 2.8 ha at Kirstenbosch on Table Mountain, 4.2 ha in Grootvadersbos near Heidelberg, 10.0 ha near Diepwalle, Knysna, and lastly 7.8 ha in the Alexandria forest east of Port Elizabeth. Both the vegetation structure and the density and distribution of insects vary somewhat among the five sites: mean vegetation height from a low of 22 m in Alexandria to a high of 28 m in Knysna, area under the foliage profile from a low of 40.1 units in Alexandria to a high of 82.6 at Kirstenbosch, and mean insect densities caught on Tanglefoot boards from a low of 7.4 insects per plaque per day at Grootvadersbos and Knysna to a high of 13.5 at Riviersonderend. Yet these forests are generally very similar in structure (see also MacKenzie 1978) and presumably also in the resources they provide for insectivorous birds. The Riviersonderend and Grootvadersbos areas were censused by Martin et al. in 1979; the correspondence in results is high, with 20 out of 22 and 23 out of 28 of my species totals respectively in their lists, and two species at each site recorded by them but not by me. Bird species totals decrease from Alexandria to Cape Town, from 42 to 15. Yet despite this nearly threefold difference in diversity, the total bird densities are extremely similar (average difference 5%, largest 11%). These figures indicate

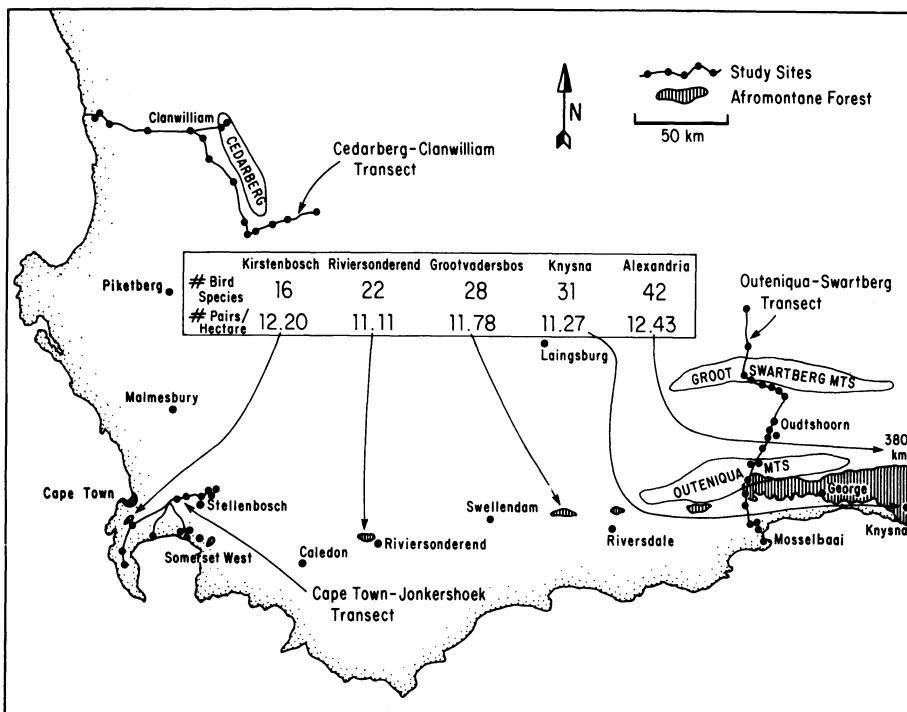


Fig. 3. Map of part of Cape Province, South Africa, showing the locations of five sites at which birds were censused in Afromontane woodland, and locations of three transects along which vegetation structure and bird diversity and density were measured.

considerable density compensation in the bird communities; the absence of bird species from the smaller and more isolated forest patches to the west, up to 65% of the Alexandria community by Kirstenbosch, is compensated by expanded foraging niches and increased densities of the remaining species.

The decrease in species numbers from Alexandria to Cape Town is very largely a filtering out of more and more species with increasing isolation, and not a process of species turnover. A few bird species with wider habitat tolerance make use of the forest habitat only towards the western end where α diversity is low. These are Serinus canicollis and Streptopelia capicola which occur in forest only from Grootvadersbos west, and Onychognathus morio and Cinnyris chalybeus, which occur in forest only from Knysna west. These species appear to be replaced by other canaries, doves and sunbirds to the east.

Density compensation is most readily observed in those species which are dominant insectivores and occur from Cape Town across to Alexandria. Zosterops pallidus decreases in density from west to east across the five sites: 2.5, 2.5, 1.5, 1.4 and 0.8 pairs ha^{-1} respectively; Muscicapa adusta with similarly decreasing densities: 1.1, 0.7, 0.4, 0.3 and 0.3 pairs ha^{-1} respectively; and Cossypha caffra, which barely makes it in forest to Alexandria: 1.0, 0.5, 0.4, 0, and 0.03 respectively. There is just one species, the insectivore Apalis thoracica, which is reasonably common in all forests east of Kirstenbosch, quite common in shorter habitats such as kloof woodland and tall fynbos near Kirstenbosch, but virtually absent from the Kirstenbosch forest. It appears that the density compensation has all gone to Zosterops, the only foliage insectivore at Kirstenbosch, to the complete exclusion of Apalis. I observed putative equilibrium densities of the four foliage insectivores at the Knysna forest of Zosterops pallidus (Z): 1.36 pairs ha^{-1} ; Apalis thoracica (A): 0.44 pairs ha^{-1} ; Seicercus ruficapilla (S): 0.94 pairs ha^{-1} ; Camaroptera brachyura (C): 1.46 pairs ha^{-1} . Competitive interactions among these four species are estimated from the overlaps between their normalized foraging height distributions using

$$\begin{array}{ccccc} & Z & A & S & C \\ \begin{matrix} Z \\ A \\ S \\ C \end{matrix} & \left[\begin{array}{cccc} 1.00 & 0.31 & 0.70 & 0.22 \\ 0.31 & 1.00 & 0.10 & 0.50 \\ 0.70 & 0.10 & 1.00 & 0.00 \\ 0.22 & 0.50 & 0.000 & 1.00 \end{array} \right] \end{array}$$

Carrying capacities at Knysna can be derived from the following equilibrium condition:

$$\begin{bmatrix} K_Z \\ K_A \\ K_S \\ K_C \end{bmatrix} = \begin{bmatrix} 1.00 & 0.31 & 0.70 & 0.22 \\ 0.31 & 1.00 & 0.10 & 0.50 \\ 0.70 & 0.10 & 1.00 & 0.00 \\ 0.22 & 0.50 & 0.00 & 1.00 \end{bmatrix} \begin{bmatrix} 1.36 \\ 0.44 \\ 0.94 \\ 1.46 \end{bmatrix}$$

whence $K_Z = 2.48$, $K_A = 1.69$, $K_S = 1.94$, and $K_C = 1.98$. We notice immediately that the carrying capacity of Zosterops at Knysna is just the equilibrium density of the species where it occurs alone at Kirstenbosch, strong evidence that we have identified the relevant competitors and that the resources are basically similar in those two forests. Yet if we remove Seicercus and Camaroptera from the four-species assembly, we predict that

Zosterops and Apalis can coexist at elevated densities via density compensation for the missing two species:

$$\begin{bmatrix} 2.48 \\ 1.69 \end{bmatrix} = \begin{bmatrix} 1.00 & 0.31 \\ 0.31 & 1.00 \end{bmatrix} \begin{bmatrix} X_Z \\ X_A \end{bmatrix}$$

whence the new equilibrium densities are $X_Z = 2.15$ and $X_A = 1.06$. Yet X_A is observed to be zero. If overall resource levels are elevated at Kirstenbosch by a factor P , then the observed equilibrial densities should be equally enhanced by the factor P . I know that the insect densities are very similar, but carrying capacity for Zosterops might be increased at Kirstenbosch by more available fruit, and by Zosterops' shifting its foraging niche from that at Knysna. If the carrying capacity of Zosterops at Kirstenbosch is in fact changed by a factor k , then

$$\begin{bmatrix} 2.48k \\ 1.69 \end{bmatrix} = \begin{bmatrix} 1.00 & 0.31 \\ 0.31 & 1.00 \end{bmatrix} \begin{bmatrix} X_Z \\ X_A \end{bmatrix}$$

Solving for equilibrium density of Apalis by Cramer's Rule,

$$X_A = \frac{\begin{vmatrix} 1.00 & 2.48k \\ 0.31 & 1.69 \end{vmatrix}}{\begin{vmatrix} 1.00 & 0.31 \\ 0.31 & 1.00 \end{vmatrix}} = 1.87 - 0.85k$$

Thus Zosterops can exclude Apalis from the Kirstenbosch forest if it can exploit new resources or shift its foraging niche and thus its carrying capacity there by a factor ($1.87/0.85$) of just over two.

Alternatively, Zosterops might exclude Apalis from the Kirstenbosch forest by niche shifts that increase the competition coefficient α_{AZ} above 0.31. In that case

$$\begin{bmatrix} 2.48 \\ 1.69 \end{bmatrix} = \begin{bmatrix} 1.00 & 0.31 \\ \alpha_{AZ} & 1.00 \end{bmatrix} \begin{bmatrix} X_Z \\ X_A \end{bmatrix}$$

at equilibrium, whence

$$X_A = \frac{\begin{vmatrix} 1.00 & 2.48 \\ \alpha_{AZ} & 1.69 \end{vmatrix}}{\begin{vmatrix} 1 & 0.31 \\ \alpha_{AZ} & 1.00 \end{vmatrix}} = \frac{1.69 - 2.48 \alpha_{AZ}}{1 - 0.31 \alpha_{AZ}}$$

If the competitive effect of Zosterops on Apalis were increased to $\alpha_{AZ} = 1.69/2.48 = 0.68$, slightly more than double 0.31, then at equilibrium X_A would be zero. These questions are discussed in more detail elsewhere (Cody 1982) and have received some theoretical attention. The likelihood and stability of alternative equilibria in multispecies competition communities are known from simulation (Case and Casten 1979). Its importance to us here is that communities that are lower in α diversity because of habitat patchiness or isolation may be subjected to additional (internal) factors that will further reduce α diversity.

20.4.3 SPECIES TURNOVER WITHIN A HABITAT BETWEEN DIFFERENT REGIONS

When a given habitat is fragmented into patches or sections that are separated by either physical barriers (e.g. cordilleras or water bodies) or on a more local level by intervening habitat of a different type, then there arises the possibility that different species might fill similar ecological roles in different parts of the range of the habitat. These ecological vicars or ecological analogues constitute a third diversity component that I call γ diversity (γ for "geography"). Here the species turnover is independent of habitat differences and is measured over geographic area within a given habitat type, H .

In the Afromontane woodland censuses discussed above there are few replacements of ecological counterparts between sites. One reason might be that as recently as 10,000 years ago many of these forest patches were contiguous or nearly so such that there would have been more interchange of birds between them. Although now there is circumstantial evidence of genetic isolation in the bulbul Andropadus importunus populations, whose songs vary little within but considerably between the western forest patches, there are no indigenous species or races there.

If ecological counterparts each occupy habitats that differ markedly in area, then the species in the more restricted area is likely to be replaced, over time, by that of the larger habitat as long as the geographic isolation of the two areas does not preclude some threshold level of immigration. Thus the point at which ecological analogues replace each other on the map should be affected by the relative areas of habitats on H (see Trombulak and Cody 1980).

Examples of γ diversity in fynbos and related vegetation are discussed below; others are to be found among flycatchers (Batis), sugarbirds (Promerops), seedeaters (Serinus), robins (Erythropygia) and rock-thrushes (Monticola).

20.5 Ecological biogeography and convergent evolution

20.5.1 EVOLUTION OF GAMMA DIVERSITY

In this section of the paper I deal with concepts necessary for understanding firstly, continental diversity patterns and secondly, convergent and non-convergent evolution. These subjects are closely related, since the major unknowns in continental diversity patterns are those factors that control γ diversity, and it is between γ diversity counterparts that we expect to see the products of convergent evolution.

A basic fact of ecological biogeography is a statement such as: Species X_1 occurs in region R_1 where it occupies habitats $f_1(H)$ in which it pursues a certain ecological role. Juxtaposed with this fact might be a second statement: X_1 fails to occur in region R_2 . As ecological biogeographers, we want to know why.

Perhaps the two statements can be reconciled because there is no suitable habitat in R_2 . Unless some part of $f_1(H)$ is represented in the second region, then we do not expect X_1 to occur there in the first place. But if $f_1(H)$ includes habitat present in R_2 , then perhaps the absence of X_1 is explained in terms of access. X_1 may be excluded by major physical barriers such as oceans or mountain chains or by biotic barriers such as very different habitat; these biotic barriers might be inhospitable per se such as a desert for woodland birds or inhospitable because of competitor species that live in the habitat barrier. If there

is no obvious barrier then we must look to the habitats $f_1(H)$ in R_2 for the explanation. The answer may be simple competition in the form of a single species X_2 , the ecological counterpart of X_1 . X_2 might be quite unrelated to X_1 in which case its role as ecological counterpart or γ diversity counterpart is a product of convergent evolution. Alternatively regions R_1 and R_2 might have been divided by a physical or biotic barrier in the past, and the two species have a recent common ancestor. Sets of γ diversity counterparts in this category were mentioned above.

If no single ecological counterpart prevents access to R_2 by X_1 , perhaps diffuse competition is the answer. Communities structured by competition may have alternative stable equilibria, some of which might include X_1 and some not. In this case the presence of several competitor species jointly serve to exclude X_1 . Again, this competition has several aspects, for close competitors might be species either with intolerably large ecological overlap with X_1 or might be species that have a larger carrying capacity in R_2 than in R_1 where they coexist with X_1 . The case of Zosterops and Apalis in Kirstenbosch could have this explanation.

Another possibility is that despite the duplication of f_1 habitats in R_2 and the absence of strong competitors, resources in these habitats might differ. Resources and consumers can coevolve tight and specific interrelations that subordinate the effects of habitat structure. If X_1 feeds only from flowers with 25-28 mm corollas or eats only hard seeds of diameters 7.5-8.6 mm, then we must be sure that such resources are present in R_2 before we wonder at X_1 's absence.

And finally the constraints of resources, access and competitors might all be satisfied, yet the areal extent of f_1 habitats in R_2 might be very small. X_1 is unlikely to persist in such small patches, and even though it might occasionally reach and use these patches we might not find it there at a given time. There are other but less tangible or less interesting possibilities why X_1 is restricted to R_1 . One might be the evolution of a sedentary tendency in X_1 such that it does not even try to reach R_2 , or strange new predators eat it when it arrives, or perhaps X_1 needs the social facilitation of its home population; for small, mobile birds oriented towards resource competition, these possibilities seem distant.

20.5.2 FIGURE 4: EFFECTS OF HABITAT PATCHINESS

Figure 4 is an attempt to clarify my perspective of some of the factors that influence continental species diversity and involves many of the foregoing concepts. I imagine that subject species X occupies a geographic range G , but within this range is able to occupy only those habitats where $H > 0.5$ and does rather poorly in habitats $H > 1.5$. Within G I have drawn contours of H showing where there is occupiable habitat. The largest habitat block is at (a) where X concentrates its $f(H)$ around $H = 1$. Other species restrict X to this range of habitats from below and above on H . Here X 's food niche F can be translated into a density, distributed over H as indicated by the hatched lines. X has access to habitats in block (b) but because habitats here are commoner in the range $H > 1.5$, X is subjected to stronger competition from the species of taller vegetation and it shifts its $f(H)$ lower on H . This in turn affects the availability of foods to which its morphology and behaviour are best suited, and thus its density is less in lower H .

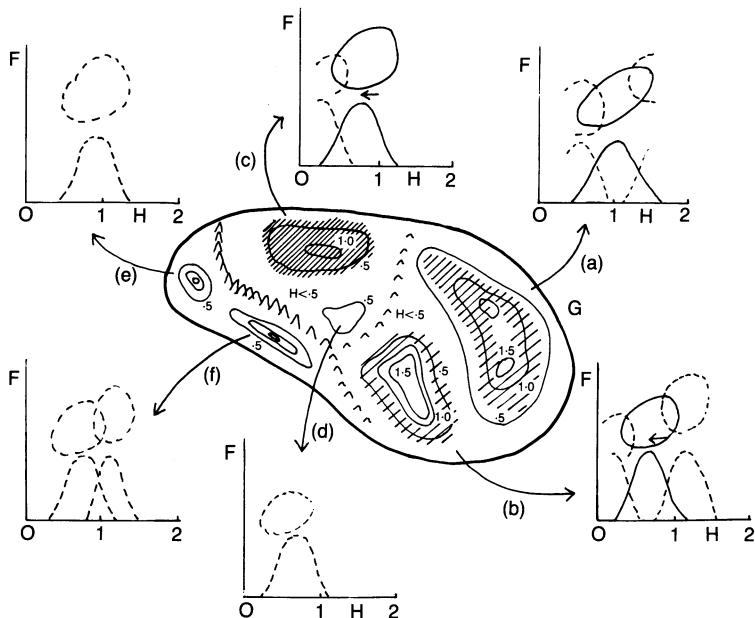


Fig. 4. Schematic representation of the availability of habitat type H, patchily distributed over a geographic region G. Contours represent changing habitat H; hatched lines and frequency distributions on the inset graphs show habitat occupancy of a given species, which changes as does habitat availability. A second niche axis F represents foraging ecology, relative to competitor species (dashed lines).

A third but smaller habitat block (c) is also colonized by X, and here the high-H competitor is absent. Thus X can both occupy all of $H > 0.5$ and make up for the missing competitor over median H values. Its density in (c) is thus high; this in turn might enable X to push more strongly into lower habitats, to which it might become somewhat better adapted by virtue of the small area and relative isolation of (c) from (a) and (b). There is also accessible habitat in patch (d) where $H > 0.5$, but the patch is too small for X to inhabit regularly, and species from the surrounding lower-H habitat annex the patch and its resources. Two additional patches of suitable habitat occur on the edge of X's range, but these are rendered less accessible by the presence of a barrier. Either patch might be invasible for X, depending on the extent to which the species that use X's resources and habitats in its absence evolve to become close ecological counterparts. With reduced accessibility of these patches to X, the time necessary for this convergent evolution is better assured.

20.5.3 EVOLUTION OF NON-CONVERGENCE

At this point I wish to restate some of the major problems in studies of convergent evolution. The important message from physiological plant ecology for bird ecologists is that soils differ in the sorts and amounts of nutrients they provide for plant growth, and these differences have been part of the evolutionary scene for millions of years. Thus plants differ in their life histories, in the rates at which they fix carbon, replace

leaves, in their defence budgets and in their modes of reproduction. In many respects the typical fynbos Protea and the typical chaparral Ceanothus are at opposite poles, with the former using a few, thick, unpalatable and long-lived leaves, producing copious nectar to attract large vertebrate pollination vectors and setting a few very large seeds. The latter has many smaller, edible and often augmented leaves, is bee-pollinated and produces many smaller seeds that are of much less significance in its population cycle. Thus despite the similar climate of fynbos and chaparral, insects and insectivorous birds are scarcer in fynbos and nectarivorous birds are scarcer in chaparral.

The importance of coevolution between resources and consumers has not been accorded the attention it deserves, and recent (unpublished) papers by A V Milewski point this out. In particular the resources that plant parts constitute for seed-, fruit-, leaf- and nectar-eating birds, and the consumers of these resources, interact to provide reciprocal feedback that affects the course of each other's evolution. Especially where these interactions are mutual, as in pollination and seed dispersal, and where it behoves both the plant and its helpful consumer to preclude the involvement of other consumers, then the two halves of the system may together trace a divergent and distinct evolutionary pathway unlikely to have a counterpart elsewhere. To some extent we can control for this effect in different communities by more accurate measurement of kinds of resources and how they differ between continents. In this way our expectations of convergence will be more modest and realistic.

The other variable I have stressed is the ecological and biogeographic consequences of habitat areas. Habitat area and the extent to which it is patchy or continuous strongly affects α and β diversity. We cannot expect to find close ecological counterparts in communities that differ in α diversity by factors of two or more as in the woodlands discussed earlier, and clearly there will be little one-to-one correspondence between the species in such communities.

We cannot control for differences in habitat area very easily, but we can at least conduct studies that will elucidate the role of habitat area and contiguity in diversity. Moreover there is a large and varied category of events and circumstances generally referred to as "historical factors" of which our understanding is even poorer. These may be short-term, and include such varied effects on diversity as the date of the last fire, the last time pipe-wood was removed from the macchia, or the last time natural browsers were present. They may also be the sorts of factors that affect speciation, the long-term contiguity and subdivision of habitats, the shifts over the map of a particular habitat type with changing climate to alter its relative accessibility from a source region, and even changes in the maps themselves. Clearly we are hardly able to ask the appropriate sorts of questions of these factors, and even further from the answers that bear on convergent evolution.

20.6 Bird diversity in three areas of Cape Province

20.6.1 SITES, DATA COLLECTION, HABITAT ORDINATION

For further insights into the interrelations among α , β and γ diversity in South African birds I studied three areas of the Cape Province in which a similar sequence of habitats was assessed for vegetation structure and over which bird diversity and density were measured. These three areas are in the Cape Town-Jonkershoek region, the Clanwilliam-Cederberg area to the

north-west, and the Outeniqua-Swartberg area in the southeastern part of the province (Fig. 3). These study sites and their characteristics are listed in Appendix B. For the Cape Town area I use the 13 sites reported in Cody (1975), located between the Cape Peninsula and the Jonkershoek valley. These sites cover a sequence of habitats between the Cape Flats in coastal strandveld to renosterveld, fynbos, kloof woodland and finally the patch of Afromontane woodland on the side of Table Mountain at Kirstenbosch. In the Cedarberg-Clanwilliam area I collected data from 2-22 October 1979 in strandveld vegetation, in renosterveld and fynbos in the Cedarberg, and in sites in karoo, karoid broken veld and succulent karoo (14 sites). I selected 17 sites in the Outeniqua-Swartberg area and worked on them from 3 November to 12 December 1979. These are located between the coast near Mosselbaai north across the Outeniquas at Robinson Pass, near Oudtshoorn and across Swartberg Pass to Prince Albert in the Karoo. The sites include coastal renosterveld and valley bushveld near the coast, mountain renosterveld and fynbos in both mountain ranges, various types of karoid vegetation in the Little Karoo and north of Swartberg, kloof woodland near Robinson's Pass, and Knysna forest at Diepwalle, north of Knysna. In general climatic variation is as great within as between transects. Rainfall on the Outeniqua-Swartberg transect shows at least a four-fold variation (George: 851 mm yr⁻¹, Oudtshoorn: 237 mm yr⁻¹); Clanwilliam is similar to Oudtshoorn with 203 mm yr⁻¹, Stellenbosch with 704 mm yr⁻¹ approaches the George total. Nevertheless, wetter sites increase from the northwestern to southeastern Cape Province, and the incidence of summer rainfall follows the same trend.

Vegetation measurements. Each site consisted of relatively homogeneous and undisturbed vegetation; although site areas are variable, from a low of 0.74 ha to a high of 30.1 ha, over one half of the sites are within the range 2-5 ha (see Appendix B). Site area was determined by the extent and continuity of the vegetation, and by bird density and distribution: taller, denser habitats with high bird density, especially those such as kloof woodland that occur naturally as patches, were sampled over small areas, while low, open and continuous vegetation with low bird density, such as the karoo sites, were sampled over much larger areas.

Within each delimited site 25 points were chosen haphazardly, and from each point orthogonal axes were established oriented according to the direction of the sun from the observer. Vegetation densities were then measured, using the inverse of the distance from the observer to points of 50% vegetation cover, along each of the four axes at a series of height intervals: 0.15 m, 0.30 m, 0.60 m, 1.2 m, 2 m, 3 m, 4 m, 6 m and thence at 2-m intervals until the vegetation was exceeded. From these 100 vegetation density measures a mean vegetation profile was constructed, and from this site-specific profile the following six variables are derived: (a) $\log(ht_{.01})$, the logarithm of the height above the ground at which vegetation density falls below .01 (reciprocal of 100 feet, = 30 m); (b) $\log(1 + \frac{1}{2}ht)$, the logarithm of 10x the height at which half the vegetation density of the profile is below and half is above (the half-height of Cody, 1975); (c) $\log(ht_{.1})$, the logarithm of the height above ground where vegetation density diminishes to 0.1 (reciprocal of 10 feet, = 3m); (d) $\log A$, the logarithm of the area under the foliage profile, in units of an interval of 1 foot (= 0.3 m) on the ordinate and an interval of 0.1 (reciprocal of 10 feet, = 3.0 m) on the abscissa; (e) the ratio $\log(ht_{.01})/\log A$, a measure of the openness of the vegetation; and finally (f) $\log(2 + \frac{1}{2}d)$, the logarithm of 100x the vegetation density at one-half the vegetation height ($ht_{.01}$). The values of these six

variables for each of the 44 sites on three transects are given in Appendix B. The data on vegetation structure are used to define a habitat plane. Since my goal is to compare bird distributions and densities between the three transects, I ordinate the habitats using vegetation data alone, with no input from bird data or distributions. I use factor analysis on the vegetation data to collapse the six variables into their first two principal components. These two variables, PCI and PCII, are statistically independent, are very similarly constructed from original measurements in each of the three data sets independently, and between them account for some 80% of the overall variation in vegetation structure. The variables are derived via the following steps: (a) construct a 44 x 6 data matrix, using all 44 sites and all six vegetation variables described above; (b) normalize the columns to zero means and unit variance; (c) derive the 6 x 6 correlation matrix; and (d) calculate the eigenvectors of this matrix. The first two eigenvectors are given in Table 2, and when the data matrix is postmultiplied by these vectors, the first two principal components are produced (last two columns of Appendix B).

Table 2. First two eigenvectors used to derive the principal components of vegetation structure of sites in three areas of Cape Province.

Q1	Q2
0.387	-0.505
0.382	-0.232
0.543	-0.080
0.518	0.035
-0.265	-0.598
0.265	0.571

Bird censuses. I conducted bird censuses that were designed to answer the question: Given that a site of these vegetational characteristics in this region is surveyed at this time of year, which bird species are encountered at the site and with what frequency? The censuses do not establish which parts of a site a species uses, what its population structure is, what territorial or other social system operates in each species, what the demographics of the various populations are, or what foraging ecology a species employs. Bird census results for sites in the three areas are given in Appendices C, D and E. The species include those that foraged within the sites during my census visits, and exclude all raptors, nocturnal species, brood parasites (cuckoos and honeyguides) and aerial foragers (swallows and swifts). The great majority of these species foraged regularly within the sites and were breeding at the time of the censuses. Many species are monogamous, defended small territories vigorously, and sang consistently (e.g. Cisticola spp., Emberiza capensis, Bradypterus victorinii, Seicercus ruficapilla, Sphenoeacus afer), and from this activity their presence and density were accurately determined. A minority of species foraged in small, narrow-ranging groups (Phoeniculus, Zosterops), others are gregarious and bred outside the study sites (Spreo, Onychognathus, many doves); Euplectes is polygynous (2-3 females per male at my sites), and a variety of species are less flamboyant in their territorial activities (Stenostira, Malurus, Telophorus, Francolinus, many sunbirds). Species in these last categories are less readily counted. At just one site (no. 17, Outeniqua-Swartberg) a north-temperate migrant

Hippolais icterina, was included in the census as a regular site user.

Most sites were visited 3-6 times, and each visit lasted 2-6 hours; during a single day I censused 3-5 sites on a transect, visiting each site at different times on different days. I moved slowly through the study area, recording on a map the location and movements of each bird encountered (by sight or sound), aided by flagging tape on the vegetation at regular intervals. At most sites successive visits produced the same list of bird species, but at others some species were observed just once or twice. Some birds had wide foraging ranges of which the study site was but a small part, and an effort was made to determine what part from observations beyond the site boundaries. Around 15 hours were spent at an average site, but considerably more detailed observations were made in the fynbos (site 11) at Jonkershoek (see Cody and Mooney 1978) and in the woodland sites at Kirstenbosch (no. 13) and Knysna (no. 7, see Cody 1982).

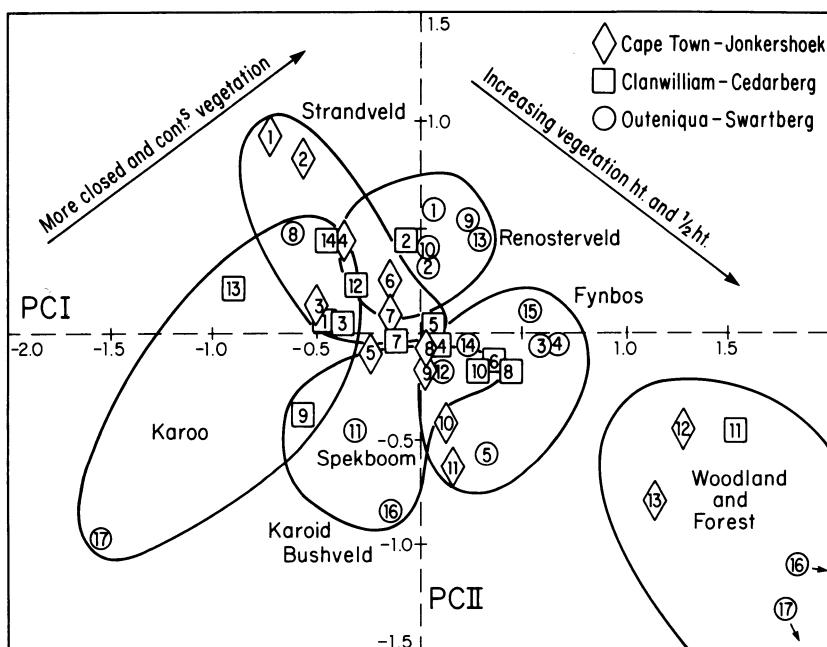


Fig. 5. Distribution of 44 sites on three transects of similar habitat, ordinated by the first two principal components of vegetation structure, PCI and PCII, which allows the sites to be represented in the habitat plane of this figure. The symbols refer to transects, and the numbers enclosed refer to the site numbers in Appendix B; the appendix lists the original habitat variables at each site, and the PCI-II figures computed for the site. Sites group according to veld type, and the axes are interpreted biologically.

At each site the census data were converted to bird density estimates in pairs ha^{-1} . These figures are given in the appendices (C-E), and while most reflect the number of breeding pairs per ha, others reflect comparable utilization of the sites by birds breeding elsewhere or at some other

time. Low density figures are obtained for those species observed only intermittently, and/or have wide foraging ranges within or beyond the study site. Although some estimates are crude, the bird density figures are used here only to compare between sites and among transects. The census data permit such conclusions as: Emberiza capensis, observed at all sites in the Clanwilliam-Cedarberg area, has a much wider habitat range there than in the other areas; Apalis thoracica is widely distributed over habitat in the Outeniqua Mountains, more restricted in the Cape Town-Jonkershoek area and, despite a range that reaches the Cedarberg, must be extremely restricted there as it was not observed at any Cedarberg site.

The sites in the Cape Town-Jonkershoek area are those of Cody (1975), but several (nos. 8, 11, 12, 13) were recensused in the last week of October 1979. The additional surveys account for some discrepancies between Appendix D of Cody (1975) and Appendix C here: add Serinus albogularis to site 8, Tersiphone viridis to sites 12 and 13, Serinus canicollis and Onychognathus morio to site 13. Anthus novaeseelandiae was omitted from site 3 and Corvus omitted for four sites in the 1975 list by error and policy respectively.

The distribution of the census sites in the plane of PCI and PCII is shown in Fig. 5. PCI correlates positively with the vegetation height and total vegetation density, whereas PCII correlates positively with high vegetation density at one-half height, and negatively with tall vegetation that is of overall low density. It is easier to interpret these axes in reference to vegetation types as named by Acocks (1975). Fig. 5 shows that the Cape Flats sites are upper left on the habitat plane, and the woodland and forest sites are to the bottom right. Between these two poles are, sequentially from the upper left, strandveld, renosterveld and fynbos. The low, sparse and open karoo sites are to the left on PCI, and the taller bushveld and karoid broken veld sites are low on PCII around the center of PCI. Each transect contributes comparable sites to most sections of the habitat plane, with the exception that no karoo sites are available on the Cape Town-Jonkershoek transect.

20.6.2 COMPARISONS OF THE BIRD FAUNAS

A total of 63 species was recorded on the Cedarberg transect, 66 species in the Outeniqua-Swartberg area exclusive of a further 17 species found in the Knysna forest, and 53 species for the Cape Town-Jonkershoek transect. Altogether 109 species were found in the combined censuses.

Some 30 species are found on all three transects, and the differences among the three lists are due chiefly to (a) a pool of eastern and/or forest species present in the Outeniqua-Swartberg area, few of which reach the Cape area and even fewer of which extend further north to the Cedarberg, and (b) a pool of northwestern and/or karoo species that fail to reach the southern and eastern habitats. Among the first category are the 17 species (see Appendix B, site 17) of the Knysna forest that show up nowhere else, and species such as Dicrurus adsimilis and Serinus scotops that extend beyond the forest but only in the Outeniquas. Other forest-associated birds that reach the Cape but are not recorded in the Cedarberg censuses are Tersiphone viridis, Andropadus importunus, Muscicapa adusta, Batis capensis, Apalis thoracica and Cisticola fulvicapilla. Twenty-six species are restricted to the Outeniqua-Swartberg transect, a further nine are shared with the Cape only, and a further 16, including many karoo species censused in the Swartberg area, are shared with the Cedarberg region only.

A small pool of eight species is found mainly on the Cape Flats and was not censused elsewhere; amongst these are Macronyx capensis, Calandrella cinerea, Cisticola textrix, Anthus novaeseelandiae and A. leucophrys. The 13 species found only in the Cedarberg area includes such karoo specialities as Oenanthe monticola and Serinus alario, and species common in strandveld and succulent karoo such as Parus afer, Batis pririt, Eremomela icteropygialis, Myrmecocichla formicivora and Melaenornis infuscatus. Clearly the location of each region has greatly influenced the species recorded in the transects despite the similarity of the habitats involved. There is an infusion of karoo and coastal strandveld species into the northwestern sites, and infusion of forest species into the eastern sites, and few of either in the Cape area where the karoo is further inland, the strandveld has almost petered out down the west coast, and the forest connection is tenuous.

20.6.3 COMPARISONS OF BIRD DIVERSITIES

Some mention has already been made of α and β diversities on the three Cape Province transects (see above, Figs 1A and 1B). I have looked at α diversity in a somewhat different light by plotting cumulative species numbers against cumulative area on the habitat plane PCI-PCII. The result confirms what was apparent earlier, that the avifauna of the Cape Town-Jonkershoek transect is somewhat depauperate in comparison to the other two. Taking nested samples from the origin of the habitat plane, an area of 1.0 on the plane produces 51 and 52 species in the Cedarberg and Outeniqua-Swartberg respectively, but only 43 species in the Cape Town area. The species-area curve for the habitat plane is worth plotting only if there is an equal density of samples over the plane from each region, and so I defer further comment until I compare specific habitat types from the three regions below.

I next analyse bird species turnover between different sites within each region. As usual I measure species turnover as the average of the number of species gained and the number of species lost from one census to another. Thus turnover from a census of five species to a census of seven species with three in common is $\frac{1}{2}(\text{no. spp gained} + \text{no. spp. lost}) = \frac{1}{2}(4 + 2) = 3$. In this way each pair of censuses on the habitat plane is characterized by a turnover value, and census sites can be grouped according to these values. In Figs 6A-C I show the contours of faunal turnover on the habitat plane for each region. These figures show clearly the extent to which there is species turnover between different habitats. In particular the contours delimit habitat sets with relatively constant bird composition (low β diversity) and those where there is high turnover (high β diversity). In the Outeniqua-Swartberg area (Fig. 6C) there are four main sets of bird species: one each in the karoo, the renosterveld and karoid broken veld, the centrally positioned valley bushveld, and the fynbos and woodland to the centre and lower right. By comparison, in the Cedarberg area (Fig. 6B) the woodland species set extends not nearly as far into the fynbos habitats in the centre of the habitat plane, there is no valley bushveld, and there is a strong segregation between the birds of the strandveld plus renosterveld and those of the karoid bushveld. Here again the karoo sites are distinct. In the Cape Town area (Fig. 6A) the fynbos and woodland sites again cluster together at low turnover levels, while the second major bird grouping is based in low strandveld with the renosterveld group annexed. These diagrams illustrate at a glance which habitats are occupied by certain cohesive faunal groups, and how these groupings shift over the habitat plane between different regions.

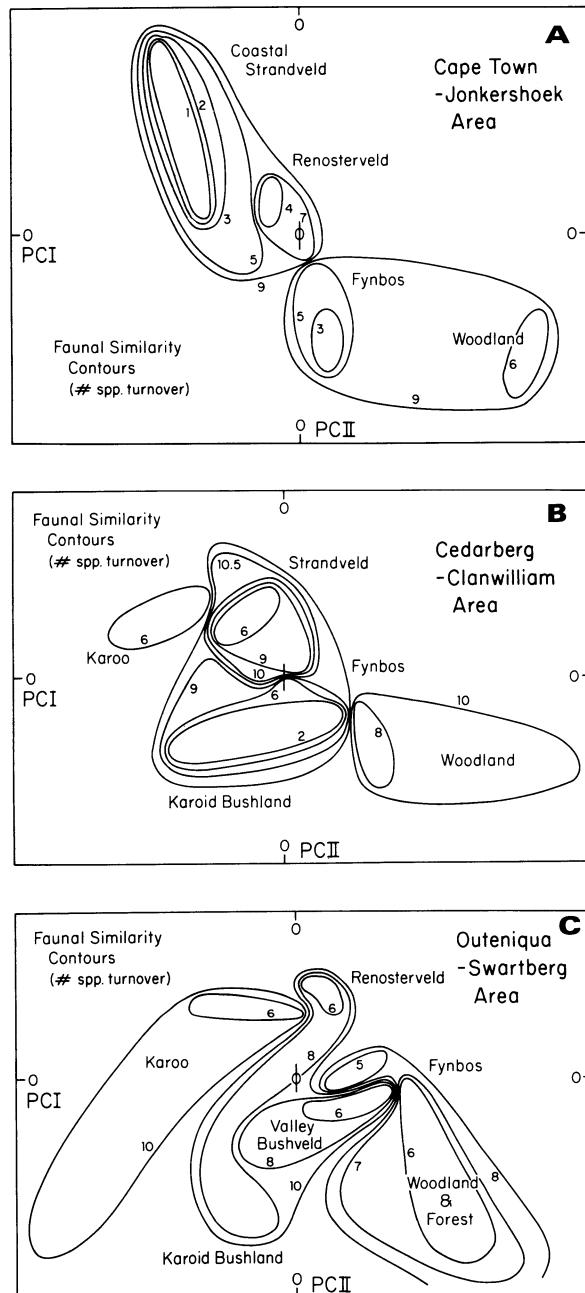


Fig. 6. Faunal similarity contours for the habitat transects. The contours include sites between which β diversity is at the magnitude indicated along the contour. Sites most similar in species lists (low β diversity) are grouped first, and the contours expanded to include additional sites that support increasingly different bird species. Thus censuses are similar within contours, but are increasingly different across contours.

20.6.4 COMPARISON OF INDIVIDUAL SPECIES DISTRIBUTIONS AMONG TRANSECTS

Next we ask to what extent do species that occur in all three regions censused occupy the same range of habitats. Taking first the ubiquitous Zosterops pallidus, its distribution on the habitat plane is shown in Fig. 7A. Not only does this species occupy a broad range of habitats, but the pattern indicates that it supports higher densities in certain habitat types from which in all directions on the habitat plane its density declines. Furthermore, there is no evidence that either the range of habitats utilized or the density in any particular habitat varies among transects. These data indicate that what is represented on the habitat plane is certainly something relevant to Zosterops. Further evidence that the habitats are arranged by combinations of variables that relate to bird habitat selection is shown in Fig. 7B where three warbler species with restricted habitat ranges are pictured. These three species are each represented several times, on two or more transects, and each occupies a discrete sector of the habitat plane.

Another widely-ranging and often abundant species is Prinia maculosa, and its distribution is shown in Fig. 7C. Apart from the one outlying point that shows the species in high density in Cedarberg kloof woodland (see below) there is little to indicate that the species occupies different habitat ranges on the three transects. However, there are differences among the densities it reaches in different regions, and in the Cape censuses Prinia numbers are double those counted elsewhere. Cisticola subruficapilla is another habitat generalist and although one cannot suggest from the data that its densities vary among transects this species occupies a more restricted range of habitats in the Cape area than it does in either of the other transects (Fig. 7D). And the last broadly distributed species considered is the bunting Emberiza capensis (Fig. 7E), recorded in all transects. This species is both more restricted in habitat range and present in lower densities in the Cape area, and reaches the highest densities where it occupies the most habitat types, in the Cedarberg.

In Fig. 7F I show the habitat distribution of Apalis thoracica, a species that favours taller and denser vegetation. It is in the eastern transect, towards the region where woodland and forest become comon habitats, that this species reaches its maximum distribution over habitat types. Here it occurs in quite low habitat in the centre of the habitat plane, habitat that is avoided in the Cape area where the species accepts nothing shorter or more open than tall fynbos. It is absent from the Cedarberg transect entirely. In Fig. 7G the distributions of two species of bulbuls are shown. That which favours forest and taller scrub habitats, Andropadus importunus, fails to reach the Cedarberg, but Pyconotus capensis occurs on all three transects. In the Outeniqua-Swartberg area (specifically in the Outeniqua censuses only) Andropadus extends its habitat range into fynbos and even renosterveld near the coast, as well as using the taller kloof woodland and forest. Pyconotus on this transect is most abundant in the open bushveld and is absent from fynbos. In the Cape Andropadus shows up only in the Kirstenbosch forest habitat, and Pyconotus is present throughout the fynbos. In the Cedarberg there are no Andropadus, and here Pyconotus extends through tall fynbos and into the kloof woodland.

Finally I show the distribution of two canary species in Fig. 8 to illustrate once more that species distribution over habitat can change markedly between different regions. In the Cedarberg the turnover point between the two species distributions occurs around $PCI = -0.25$, whereas in

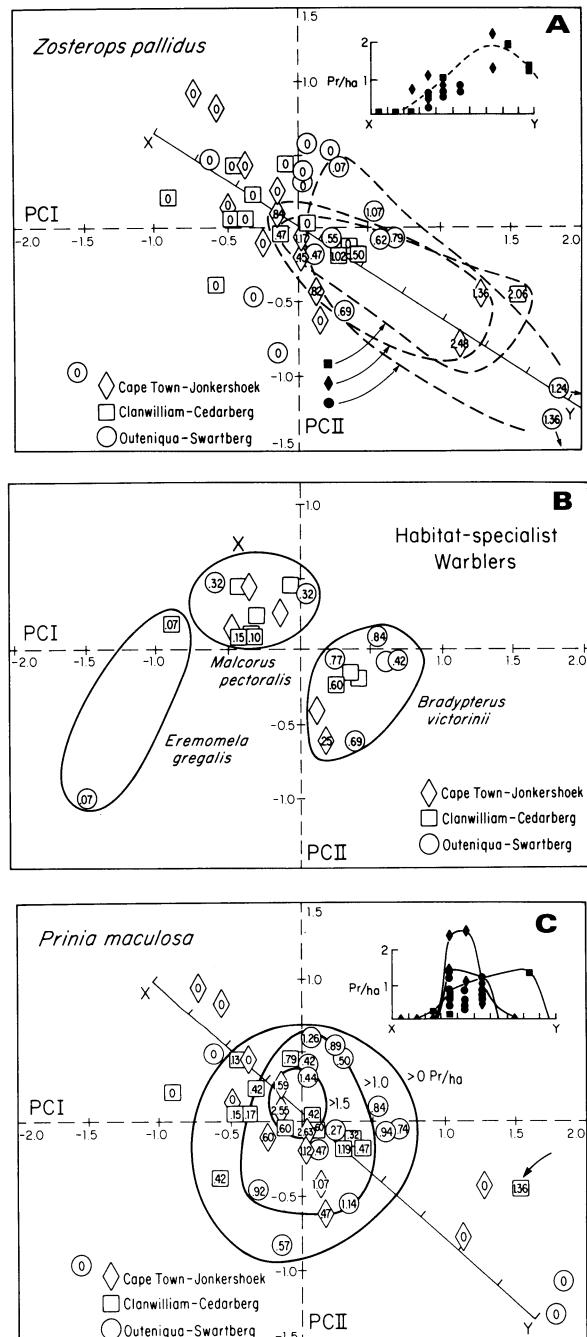


Fig. 7 (legend see p. 383)

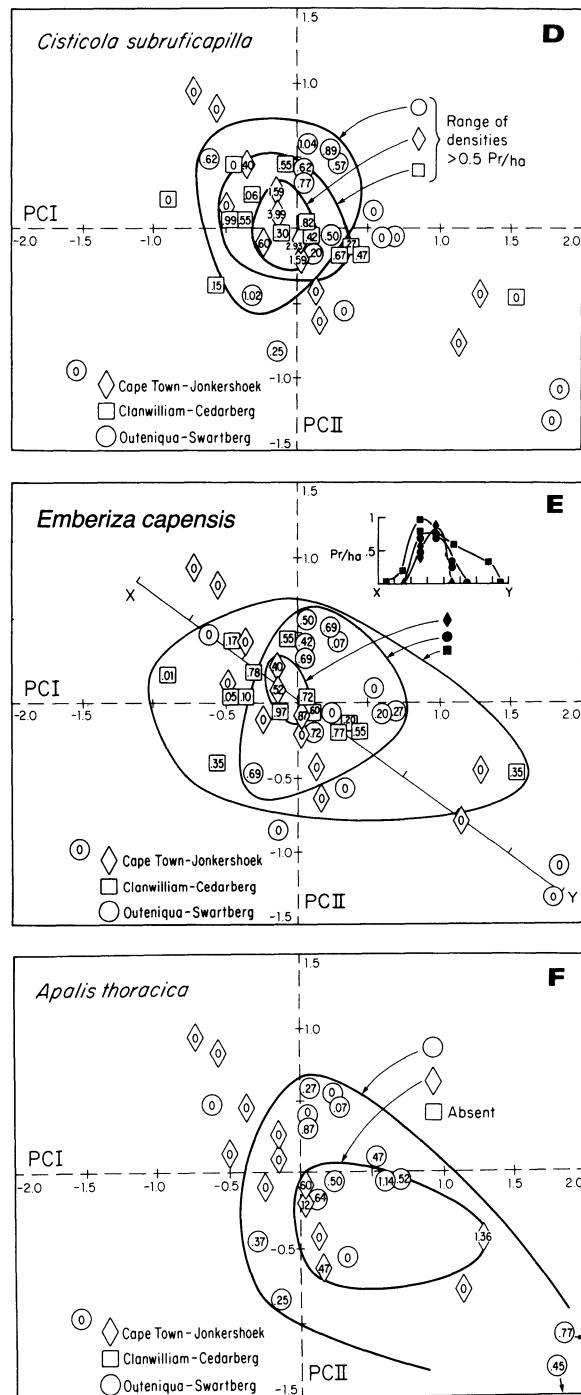


Fig. 7 (legend see p. 383)

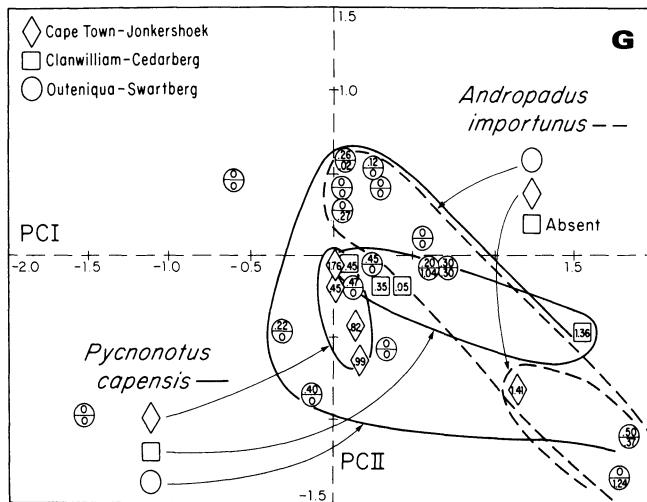


Fig. 7. Distribution of representative species in the habitat plane. The figures enclosed by the symbols are observed densities (pairs ha^{-1}). The white-eye (*Zosterops pallidus*) (A) is a species of tall fynbos and woodland, and shows no appreciable differences in either the range of habitats occupied or the densities it reaches in comparable habitats among the three transects. The three warbler species shown (B) are restricted in the habitats they occupy, with the karoo green warbler at left, the rufous-eared warbler above, and Victorin's scrub warbler to the right. Each is patchily distributed within a narrow range of habitats; empty symbols indicate absence from censused habitat. The karoo prinia (*Prinia maculosa*) (C) is a broadly distributed species that occupies all sites within its habitat range. Its range differs little among transects; densities of prinias are highest in the centre of its habitat range, but are also higher in the Cape Town area, and in taller habitat in the Cedarberg. The grey-backed cisticola (D) is a warbler that occupies a narrower habitat range in the Cape Town-Jonkershoek region and a wider range in the Clanwilliam-Cedarberg area compared to that of the third and intermediate region. Cape buntings (*Emberiza capensis*) (E) have both a narrower habitat range and lower densities in the Cape Town area, and occupy a broader habitat range at higher densities in the Cedarberg. The warbler (*Apalis thoracica*) (F), occupies a large habitat range in the Outeniqua-Swartberg area where its preferred habitats, tall scrub and woodland, are common, a reduced range in the Cape Town area, and was not found at sites in the Cedarberg area where its preferred habitat is rare. Cape bulbuls (*Pycnonotus capensis*) (G) were censused on all three transects, but are variable in their habitat ranges among transects. Sombre bulbuls (*Andropadus importunus*) are absent from the Cedarberg, occur only in tall woodlands in the Cape Town area, but occupy a wide range of habitat in the Outeniqua-Swartberg region.

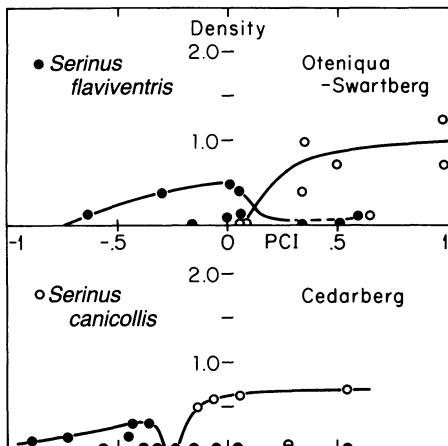


Fig. 8. The yellow canary (*Serinus flaviventris*) is found in shorter and more open habitats than the Cape canary (*Serinus canicollis*) but the turnover point between the two differs between the Cedarberg and the Oteniqua-Swartberg.

the Oteniquas and Swartberg it is around $\text{PCI} = 0.15$. This case is particularly interesting, for since *S. canicollis* is the species of taller and denser vegetation, one might predict that it would push the second species, *S. flaviventris*, into shorter vegetation where it is at a habitat-area advantage in the east, and the reverse would happen in the Cedarberg where shorter vegetation predominates. In fact the reverse happens; perhaps the presence of *S. scotops* in even taller (eastern) habitat might be involved, but the example does show that we understand poorly the factors that control species turnover on habitat gradients.

20.6.5 COMPARISON OF THREE SPECIFIC HABITATS BETWEEN TRANSECTS

Renosterveld. Unlike other habitats renosterveld is both widely distributed over the Cape Province and is dominated by a single low shrub, *Elytropappus rhinocerotis*. The habitat provides a relatively constant vegetation structure, and because it is so widespread hundreds of bird species must have access to it. It is instructive therefore to compare the bird communities of renosterveld in four sites: site 6 in Devon Valley of the Cape transect, site 1 near Hartenbos in the Oteniquas, site 13 in the Swartberg and site 2 at Kromrivier in the Cedarberg. Note that these sites are adjacent on the habitat plane (Fig. 5).

All four sites are similar in γ diversity, with 14, 13, 15 and 14 species. Yet a total of 27 bird species is found on the four sites, and consequently there is a considerable species turnover between sites. This is γ diversity, measured again as the average number of species gained and lost between censuses, and values are obtained as shown in Table 3. Here two values for γ diversity are given, the first taking account simply of species names, and the second of the densities of these species. Computation of this second figure is straightforward: if census 1 has a total of 8 pairs ha^{-1} , and census 2 a total of 9 pairs ha^{-1} , and the species in common have a summed density of 5 pairs ha^{-1} (using the lower density figure of the two values from the two sites) then the turnover in

bird density is $\frac{1}{2}(4 + 3) = 3.5$ pairs ha^{-1} . Table 3 shows that species turnover is 5-8 species between different renosterveld censuses, and density differences are greater between the Cape and the other sites.

Table 3. Gamma diversities of species numbers and species densities ($pairs\ ha^{-1}$) in three habitat types among four areas of Cape Province. ♦ = Cape Town-Jonkershoek, ○ = Outeniqua Mountains, ● = Swartberg and ■ = Cedarberg

Habitat	Transects compared					
	♦-○	♦-●	♦-■	○-●	○-■	●-■
RENSTERVELD						
Species:	6.5	5.5	5.0	8.0	7.5	6.5
Density:	3.5	4.2	3.7	2.5	2.5	2.2
FYNBOS						
Species:	7.0	7.0	8.0	9.0	16.0	14.0
Density:	4.5	4.6	6.1	3.0	4.0	4.5
KLOOF WOODLAND						
Species:	4.5	---	6.0	---	7.5	---
Density:	3.8	---	7.9	---	7.7	---

Gamma diversities of 5-8 spp. between sites are misleading in that they do not account for the relative abundances of the species in question. In fact the renosterveld bird communities are similarly composed and organized in that they share core or dominant species with similar relative abundances (Table 4). There are five spp. present at every site, and these shared species account for between 55 and 70% of the total bird density. In Fig. 9A I have plotted cumulative relative abundance of the "core" species against their cumulative rank order overall, adding to the commonest species (*Prinia maculosa*) the second commonest (*Cisticola subruficapilla*) and so on, and I find that a set of eight commonest species, species that occur in at least three of the four sites, account for between 65% and 72% of the total bird densities. Thus I conclude that these communities share the same basic organization.

There remain two ways in which the communities differ. Firstly, there are 5-7 species that differ between censuses; but these are peripheral species using a minor proportion of the birds' resources. Secondly, there are major differences in total bird densities among sites (factor of almost four). This illustrates again that matching vegetation structure assures a reasonable match in α diversity, but does not control for bird density. It remains untested that food resources differ in abundance between sites, perhaps in response to rainfall differences, and that in consequence bird densities differ accordingly.

Fynbos. In each of four ranges, Cedarberg, Jonkershoek, Outeniquas and Swartberg, I select two fynbos sites, one that is more open and dominated by *Protea nitida*, and the other a more closed and dense vegetation dominated by other *Protea* spp. These sites are nos. 10 and 11 in Jonkershoek, 4 and 5 in the Outeniquas, 7 and 10 in the Cedarberg and 14 and 15 in the Swartberg. These censuses comprise the basis for a comparison of fynbos bird communities in the four different regions (see Table 5). Looking first at γ diversity, the values for species turnover

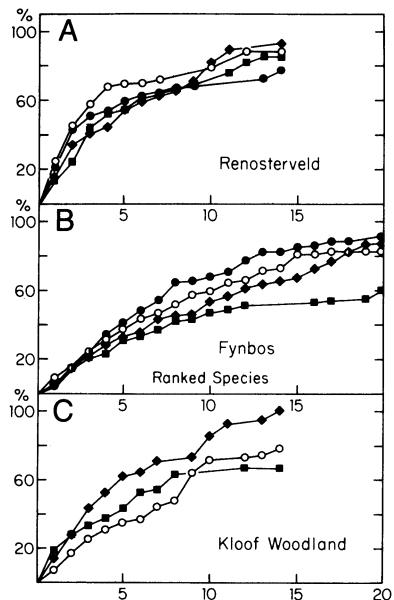


Fig. 9. For three habitat types, (A) renosterveld, (B) fynbos and (C) kloof woodland, species are ranked in order of decreasing density (abscissa). The curves show that the cumulative total bird density of these ranked species is similar among transects for the first two habitats, especially in renosterveld. Symbols are as before, with Outeniqua open and Swartberg closed circles.

Table 4. Renosterveld censuses at four sites in Cape Province.

Ranked bird species	Densities (pairs ha ⁻¹) and cumulative percentages			
	Cape Town-Jonkershoek	Outeniqua	Swartberg	Clanwilliam-Cedarberg
<u>Prinia maculosa</u>	1.59(15%)	1.26(23%)	0.50(20%)	0.79(15%)
<u>Cisticola subruficapilla</u>	1.59(34%)	1.04(42%)	0.57(45%)	0.55(25%)
<u>Erythropygia coryphaeus</u>	0.69(36%)	0.62(54%)	0.15(49%)	0.94(43%)
<u>Emberiza capensis</u>	0.40(46%)	0.50(63%)	0.07(52%)	0.55(53%)
<u>Streptopelia capicola</u>	0.99(57%)	0.07(64%)	0.17(59%)	0.12(55%)
<u>Streptopelia senegalensis</u>	0.40(61%)	----(64%)	0.05(61%)	0.40(63%)
<u>Nectarinia chalybea</u>	0.40(66%)	0.07(66%)	0.07(64%)	----(63%)
<u>Telophorus zeylonus</u>	0.30(69%)	----(66%)	0.07(67%)	0.12(65%)
<u>Francolinus</u> spp.	0.40(73%)	----(66%)	----(67%)	0.07(67%)
<u>Serinus flaviventris</u>	0.99(84%)	0.42(73%)	----(67%)	----(67%)
<u>Euplectes capensis</u>	0.79(92%)	----(73%)	----(67%)	0.55(77%)
<u>Nectarinia famosa</u>	----(92%)	0.42(81%)	----(67%)	0.27(82%)
<u>Mirafr'a apiata</u>	----(92%)	----(81%)	0.07(70%)	0.27(87%)
<u>Numida meleagris</u>	0.20(96%)	----(81%)	0.12(75%)	----(87%)
Additional species:	2	5	5	3
Total bird species:	14	13	15	14
Total bird density:	9.24	5.42	2.47	5.32

and density turnover are given in Table 3. The Cape sites, with their position intermediate between the northern Cedarberg and the eastern Outeniquas and Swartberg, are about equally dissimilar (or similar) to both, a 7-8 spp. difference. A similar difference distinguishes the Outeniquas from the Swartberg, but the Cedarberg and the Outeniqua-Swartberg have twice this γ diversity. In terms of density turnover, all six comparisons are roughly similar.

The γ diversity figures again reflect the fact that many species can occur in fynbos in very low density, and generally these rarer species are different from one region to another. Yet the important core species are those that occur both in high density and in all four areas. This is shown in Table 5 and Fig. 9B. Although a total of 55 species are listed at the eight sites under consideration (two sites in each area), a small proportion of these constitute a major proportion of the total fynbos bird density. Species are ranked according to overall abundance in Table 5. Some thirteen species occur at all four localities, including four foliage insectivores (nos. 1, 3, 6 and 9 in the list) and two nectarivores (nos. 2 and 4 in the list). A robin, finch, dove, shrike, bulbul, widow-bird and francolin complete the list of ubiquitous species (listed nos 5, 7, 8, 11,

Table 5. Fynbos censuses at four sites in Cape Province.

Ranked bird species	Densities (pairs ha ⁻¹) and cumulative percentages			
	Cape Town-Jonkershoek	Outeniqua	Swartberg	Clanwilliam-Cedarberg
<u>Prinia maculosa</u>	0.77(06%)	0.94(10%)	0.56(06%)	0.90(09%)
<u>Promerops cafer</u>	0.63(11%)	0.54(16%)	0.95(15%)	0.51(14%)
<u>Zosterops pallidus</u>	0.83(17%)	0.74(24%)	0.81(23%)	0.75(21%)
<u>Nectarinia violacea</u>	0.96(24%)	0.65(31%)	1.02(33%)	0.42(25%)
<u>Cossypha caffra</u>	0.58(29%)	0.65(38%)	0.67(40%)	0.75(33%)
<u>Sphenoeacus afer</u>	0.67(34%)	0.57(44%)	0.79(47%)	0.34(36%)
<u>Serinus canicollis</u>	0.72(39%)	0.26(47%)	0.60(53%)	0.34(40%)
<u>Streptopelia capicola</u>	0.47(43%)	0.39(52%)	0.39(57%)	0.38(43%)
<u>Bradypterus victorini</u>	0.13(44%)	0.56(58%)	0.81(65%)	0.30(46%)
<u>Nectarinia famosa</u>	0.88(51%)	0.23(60%)	----(65%)	0.34(50%)
<u>Laniarius ferruginea</u>	0.46(54%)	0.39(64%)	0.14(67%)	0.13(51%)
<u>Pycnonotus capensis</u>	0.91(61%)	0.15(66%)	0.23(69%)	0.18(53%)
<u>Cisticola subruficapilla</u>	0.21(63%)	0.51(72%)	0.71(76%)	----(53%)
<u>Onychognathus morio</u>	0.66(68%)	----(72%)	0.16(77%)	0.26(55%)
<u>Euplectes capensis</u>	0.20(69%)	0.26(74%)	0.36(81%)	0.18(57%)
<u>Apalis thoracica</u>	0.24(71%)	0.26(77%)	0.49(86%)	----(57%)
<u>Serinus leucopterus</u>	0.60(76%)	----(77%)	0.37(89%)	----(57%)
<u>Francolinus spp.</u>	0.60(80%)	0.10(78%)	0.10(90%)	0.14(60%)
<u>Batis capensis</u>	0.34(83%)	0.58(85%)	----(90%)	----(60%)
<u>Serinus sulphuratus</u>	0.64(88%)	0.08(85%)	----(90%)	0.09(61%)
<u>Nectarinia chalybea</u>	----(88%)	0.16(87%)	0.14(91%)	0.42(65%)
Additional species:	5	8	7	22
Total bird species:	25	27	25	39
Total bird density:	13.11	9.20	10.13	10.44

12, 15 and 18 respectively). Additional species of foliage insectivores (nos 13, 16), sunbirds (nos 10, 21), a starling (no. 14) and a finch (no. 20) occur at three localities. Cumulative percentages of total species density, of species in the rank order given, remain within 15% of each other throughout the cumulative ranking, and end within 3% of each other in the first three comparisons. The Cedarberg sites are somewhat different (39 versus 25-27 species), and have 22 other species that comprise a combined one-third of the total bird density.

The outcome, as seen in Fig. 9B, is that fynbos communities in different regions have the same basic constitution, the same species with the same relative abundances, over at least the first 50-60% of their bird numbers and densities. The 21 spp. ranked in Fig. 9B total between 65% and 91% of the total bird density. The other 34 species are best termed peripheral species, and their occurrence in fynbos seems an artifact of the character of the surrounding habitat and its extent. For example, the foliage insectivores Cisticola fulvicapilla and Apalis thoracica were not found in fynbos in the Cedarberg area; both species become much rarer in lower habitat of the sort that surrounds the Cedarberg. These species are fifth and sixth in abundance among the foliage insectivores, and there are insectivores in the Cedarberg fynbos, such as Sylvietta rufescens, Parisoma subcaeruleum and P. layardi, characteristic of shorter habitat that fill a comparable role as auxiliary foliage gleaners. In a similar way, the core dove of the fynbos is Streptopelia capicola, and whereas in the Cape and Outeniqua areas it is backed up by Streptopelia semitorquata typical of taller and denser habitat, in the Cedarberg the backup role is played by Oena capensis and Streptopelia senegalensis, both typical of lower and more open habitat.

I have recorded 10 species of seed-eating birds in fynbos, but only two of these are listed in the core species list, Euplectes capensis and Serinus canicollis. Of the remainder, many species appear to be opportunistic in their use of a particular patch of fynbos. I recorded Serinus sulphuratus and Serinus leucopterus in Jonkershoek, the former plus Serinus albogularis in the Cedarberg, the former again plus Serinus gularis in the Outeniquas, and just Serinus leucopterus in the Swartberg. The largest category of peripheral species is that of the open-country ground-foraging omnivores that enters fynbos in the Cedarberg. Besides the two core species, Cape robin and boubou shrike, there are starlings, chats, shrikes, larks and robins, all typical of lower and drier habitat, and occurring unpredictably in low densities in fynbos. Despite their contribution to α and γ diversity, such species are of only minor importance in the fynbos community, which in its essentials remains unchanged over many hundreds of miles of territory.

Kloof woodland Renosterveld is of very wide distribution and fynbos is of more restricted occurrence in the southern Cape Province. The habitat I consider next is of even more restricted distribution, being confined to valley bottoms where there is a permanent watercourse. Kloof woodlands were censused in the Outeniquas, in the Jonkershoek valley and in the Cedarberg; these are sites 6, 12 and 11 respectively in Appendix B. In this habitat there is more potential for dramatic differences between the bird communities, for this is the habitat that becomes abundant in eastern Cape Province and is almost nonexistent in the Cedarberg.

The species censused in the kloof woodland are given in Table 6; the totals vary from 18 in the Outeniquas to 13 in both the Cape and the Cedarberg. There is a close correspondence between Cape and Outeniquas with only two species present in the former and absent from the latter. But the Outeniqua census contains six species not present at the Cape, four

Table 6. Kloof woodland censuses at three sites in Cape Province.

Ranked bird species	Densities (pairs ha ⁻¹) and cumulative percentages		
	Cape Town-Jonkershoek	Outeniqua	Clanwilliam-Cedarberg
<u><i>Cossypha caffra</i></u>	1.56(12%)	0.99(08%)	2.75(20%)
<u><i>Zosterops pallidus</i></u>	1.36(23%)	1.24(19%)	2.06(34%)
<u><i>Laniarius ferruginea</i></u>	1.56(35%)	0.87(26%)	0.69(39%)
<u><i>Serinus canicollis</i></u>	0.97(42%)	0.62(31%)	0.69(44%)
<u><i>Turdus olivaceus</i></u>	0.97(50%)	0.62(36%)	0.69(49%)
<u><i>Streptopelia capicola</i></u>	0.25(52%)	0.25(38%)	1.36(58%)
<u><i>Nectarinia famosa</i></u>	0.67(57%)	0.74(44%)	0.17(60%)
<u><i>Batis capensis</i></u>	2.70(78%)	1.98(61%)	----(60%)
<u><i>Apalis thoracica</i></u>	1.36(88%)	0.77(67%)	----(60%)
<u><i>Pycnonotus capensis</i></u>	----(88%)	0.50(71%)	1.36(69%)
<u><i>Sigelus silens</i></u>	0.67(93%)	----(71%)	0.22(71%)
<u><i>Onychognathus morio</i></u>	----(93%)	0.25(74%)	0.69(76%)
<u><i>Tersiphone viridis</i></u>	0.45(97%)	0.45(77%)	----(76%)
<u><i>Streptopelia semitorquata</i></u>	0.27(99%)	0.25(79%)	----(76%)
Additional species:	1	5	3
Total bird species:	13	18	13
Total bird density:	12.91	12.01	14.10

of these being typical forest or woodland birds (*Andropadus importunus*, *Serinus scotops*, *Dicrurus adsimilis* and a replacement flycatcher for *Sigelus*, *Muscicapa adusta*). The Cedarberg census shares nine species with the Outeniquas, but includes in addition three species not at all typical of this woodland habitat: *Euplectes capensis*, *Prinia maculosa*, *Emberiza capensis* (and once again *Sigelus silens*). It appears that in the absence of birds more appropriate to this habitat in the Cedarberg outpost, the only patch of woodland I could find in the area, non-woodland species are able to utilize it.

The Y diversity figures between paired sites are given in Table 3. These figures are notable only to the extent that species densities vary considerably among sites. Rather surprising is the fact that the highest total bird density is observed in the Cedarberg. It appears that opportunistic species in the Cedarberg kloof are able to function very well there, a situation reminiscent of that mentioned above with island supertramps.

From Fig. 9C it is seen that, accumulating species in order of their mean abundances over the three sites, there is little correspondence in the community structure in different kloofs beyond the first four or five species and little evidence of convergent evolution in the patches. The high densities of ecologically inappropriate species in the Cedarberg kloof emphasizes the classical ecological question of the extent to which bird densities are regulated by food resources directly rather than indirectly via behavioural mechanisms.

Acknowledgements

The recent field work in South Africa reported in the paper was conducted with financial assistance from the Guggenheim Foundation, while the author was a Fellow, and from the Percy Fitzpatrick Institute of African Ornithology through the kind consideration of its director W R Siegfried. The Office of Academic Computing at the University of California, Los Angeles provided computing facilities. My wife Daryl Ann Cody helped with the field work. Peter Frost laboured to improve the manuscript, but is not sure his efforts were well spent. My colleague Hartmut Walter assisted in the collection of Sardinian bird data.

References

- ACOCKS JPH (1975) Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 40
- BROWN JH (1971) Mammals on mountaintops: non-equilibrium insular biogeography. American Naturalist 105: 467-478
- BROWN JH, KODRIC-BROWN A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449
- CASE TJ, CASTEN RG (1979) Global stability and multiple domains of attraction in ecological systems. American Naturalist 113: 705-714
- CASE TJ, GILPIN ME, DIAMOND JM (1979) Overexploitation, interference competition, and excess density compensation in insular faunas. American Naturalist 113: 843-854
- CASE TJ, CODY ML (1982) The theory of island biogeography. Chapter 12. In: CASE TJ, CODY ML (eds) Biogeography of islands in the sea of Cortez. University of California Press, Berkeley. In press
- CODY ML (1975) Towards a theory of continental diversities: bird distributions over mediterranean habitat gradients. In: CODY ML, DIAMOND JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, pp 214-257
- CODY ML (1978) Distribution ecology of Haplopappus and Chrysothamnus in the Mohave Desert. 1. Niche position and niche shifts on north-facing granitic slopes. American Journal of Botany 65: 1107-1116
- CODY ML (1980a) Evolution of habitat use: geographic perspectives. Proceedings of the Seventeenth International Ornithological Congress. Berlin. Verlag der Deutschen Ornithologen-Gesellschaft. V.II: 1013-1018.
- CODY ML (1980b) Species-packing in insectivorous bird communities: density, diversity, and productivity. Proceedings of the Seventeenth International Ornithological Congress. Berlin. Verlag der Deutschen Ornithologen-Gesellschaft. V.II: 1071-1077
- CODY ML (1981) Habitat selection in birds: the roles of vegetation structure, competitors and productivity. Bioscience 31: 107-113
- CODY ML (1982) Bird diversity and density in the afromontane woodlands of Cape Province. MS in review
- CODY ML, MOONEY HA (1978) Convergence versus nonconvergence in mediterranean-climate ecosystems. Annual Review of Ecology and Systematics 9: 265-321
- DIAMOND JM (1974) Colonization of exploded volcanic islands by birds: the supertramp strategy. Science 184: 803-806
- DIAMOND JM (1975) Assembly of species communities. In: CODY ML, DIAMOND JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge. pp 342-444

- HORN HS, MACARTHUR RH (1972) Competition among fugitive species in a harlequin environment. *Ecology* 53: 749-752
- LEVINS R (1968) Evolution in changing environments. Princeton Monographs in Population Biology, vol 2. Princeton, New Jersey. 120 pp
- LEVINS R, CULVER D (1971) Regional coexistence of species, and competition between rare species. *Proceedings of the National Academy of Science of the United States of America* 68: 1246-1248
- MACKENZIE B (1978) A quantitative and qualitative study of the indigenous forests of the southwestern Cape. MSc Thesis. University of Cape Town
- MARTIN (1979)
- MILEWSKI AV (1982) A theory of coadaptation with frugivores and nectarivores to explain differences in the vegetation of mediterranean Australia and South Africa. Unpublished MS
- ROSENZWEIG MR (1975) On continental steady states of species diversity. In: CODY ML, DIAMOND JM (eds) *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, pp 121-140
- SAHAB (1966)
- TROMBULAK S, CODY ML (1980) Distributions of Pinus edulis and P. monophylla in the New York Mountains, eastern Mojave Desert. Madrono. In press
- WHITE F (1978) The afromontane region. In: WERGER MJA (ed) *Biogeography and ecology of southern Africa*, vol 1. Junk, The Hague, pp 463-513

Appendix A. Avifauna census data for Sardinia and Corsica. "+" indicates species' presence, asterisks its absence.

Study site:	San Salvatore	Sant'Antioco	Pabillonis	Campagnasissa	Narcao	Carboneara	Bauhinia	Terebinthina	Porto Bento	Zonza
AREA(ha):	2.22	2.04	1.85	3.08	2.64	2.31	1.94	3.96	2.58	4.72
VEG. HT. (m):	0.42	0.60	0.80	0.96	1.44	2.41	2.38	3.79	7.20	9.06
VEG. #HT(m):	0.07	0.17	0.11	0.17	0.39	0.42	0.91	1.21	2.97	1.70
H:	0.054	0.251	0.327	0.420	0.630	0.820	0.885	1.067	1.375	1.399
No. SPP. GAINED:	6	9	11	14	20	26	30	38	38	40
No. SPP. LOST:										
Tot. SPP:	6	5	2.19	4.74	6.48	7.61	12.29	20.01	20.55	21.37
SPECIES: Tot. DENSITY (pairs ha ⁻¹):	2.47	2.65	5.41	9.36	7.07	8.08	8.46	13.40	15.28	18.88
1. <i>Cisticola juncidis</i>	0.45									
2. <i>Alauda arvensis</i>	0.67	**	0.74							
3. <i>Anthus campestris</i>	0.45	**		0.25						
4. <i>Calandrella cinerea</i>	0.45	0.15	4.22	2.68						
5. <i>Coturnix coturnix</i>	+	**		0.97						
6. <i>Saxicola torquata</i>	0.45	1.46	0.10	0.97	0.50	0.12				
7. <i>Emberiza calandra</i>	0.67	+	2.28	1.34	**	0.20				
8. <i>Sylvia sarda</i>	0.20	**		0.77	**	0.42				
9. <i>Sylvia melanocephala</i>	0.17	0.25	1.59	2.60	0.77	0.52	0.12	0.79	0.27	
10. <i>Melanocorypha calandra</i>	0.10									
11. <i>Sylvia conspicillata</i>	0.25	0.50	**	**	**	+	**	**	**	0.50
12. <i>Alectoris barbara</i>	0.32		0.15	0.87	**	+				
13. <i>Acantis cannabina</i>	0.50		0.15	0.87	**	+				
14. <i>Garduelis carduelis</i>	0.64	0.37	1.02	1.56	0.60	1.17	0.64			
15. <i>Emberiza cirrus</i>	0.57	0.87								
16. <i>Lanius senator</i>	0.37	0.87								
17. <i>Lullula arborea</i>	0.37	**	**	**	**	**	**	**	0.22	
18. <i>Sylvia undata</i>	0.77	0.64	2.33	0.64	+	+				
19. <i>Stereopelia tutur</i>	+	+	**	**	**	**	**	**	+	
20. <i>Parus major</i>	0.27	0.25	0.52	0.60	0.77	0.32	1.41	0.37		
21. <i>Monticola solitarius</i>	0.42									
22. <i>Merops apiaster</i>	+	+	+	+	+	+	**	**	+	
23. <i>Upupa epops</i>	+	**	+	0.42	0.52	1.46	1.74	**	**	1.84
24. <i>Sylvia cantillans</i>	0.42	0.25	0.30	0.47	0.47	0.47	0.84	1.07		
25. <i>Serinus serinus</i>	+	**	0.05	0.05	**	**	**	0.27		
26. <i>Luscinia megarhynchos</i>					0.52	0.05	**	**	0.67	
27. <i>Lanius collurio</i>					0.25	0.06	0.50	0.42	**	
28. <i>Chloris chloris</i>					0.40	0.20	0.35	1.31	0.35	
29. <i>Turdus merula</i>					0.72	0.45	0.50	0.42	**	
30. <i>Troglodytes troglodytes</i>					0.40	0.72	0.22	0.22	0.79	0.74

31. <i>Sylvia atricapilla</i>	1.17	2.23	+	1.31	0.82
32. <i>Erythacus rubecula</i>	2.93	1.36	**	1.14	2.38
33. <i>Parus caeruleus</i>	0.35	0.30	**	0.79	0.45
34. <i>Muscicapa striata</i>	0.30	1.04	0.22	0.79	0.17
35. <i>Regulus ignicapillus</i>	0.87	2.13	0.42	1.59	1.36
36. <i>Parus atter</i>	1.46	0.57	**	0.52	1.64
37. <i>Fringilla coelebs</i>	0.72	1.36	0.35	3.77	1.31
38. <i>Garrulus glandarius</i>	0.20	0.20	**	0.27	0.25
39. <i>Passer hispaniolensis</i>	+				
40. <i>Coccothraustes coccothraustes</i>	1.07	0.37			
41. <i>Parus aegithaloides</i>	0.74				
42. <i>Endrocyptus major</i>	0.62				
43. <i>Regulus regulus</i>	0.55				
44. <i>Certhia familiaris</i>	0.35				
45. <i>Sitta whiteheadi</i>	0.35				
46. <i>Columba palumbus</i>	+				

Appendix B. Site data for transects in the Cape Province. "+" indicates

Location of site	Habitat	Dominant plants
CAPE TOWN-JONKERSHOEK		
1. Gordon's Bay	Lower Cape Flats	Restiads, Asteraceae
2. Gordon's Bay	Low Cape Flats	Asteraceae, Iridaceae
3. Cape Peninsula	Coastal fynbos	Restiads, <u>Erica</u>
4. Gordon's Bay	Low renosterveld	<u>Elytropappus</u>
5. Cape Peninsula	Coastal fynbos	<u>Thamnochortus</u>
6. Devon Valley	Renosterveld	<u>Elytropappus</u>
7. Devon Valley	Tall renosterveld	<u>Elytropappus</u>
8. Swartklip	Coastal fynbos	<u>Metalasia</u> , <u>Euclea</u>
9. Jonkershoek	Low fynbos	<u>Protea repens</u>
10. Jonkershoek	Open fynbos	<u>Protea nitida</u>
11. Jonkershoek	Tall dense fynbos	<u>P. repens</u> , <u>P. nerifolia</u>
12. Jonkershoek	Kloof woodland	<u>Brabejum</u> , <u>Cunonia</u>
13. Kirstenbosch	Afromontane forest	<u>Virgilia</u> , <u>Cassine</u>
CEDARBERG-CLANWILLIAM		
1. Lambert's Bay	Low strandveld	<u>Ruschia</u> , <u>Helichrysum</u>
2. Kromrivier	Renosterveld	<u>Elytropappus</u> , <u>Berzelia</u>
3. Lambert's Bay	Succulent strandveld	<u>Ruschia</u> , <u>Cotyledon</u>
4. Kromrivier	Low fynbos	<u>Leucadendron</u>
5. Lambert's Bay	Tall strandveld	<u>Zygophyllum</u> , <u>Lycium</u>
6. Clanwilliam	Karoid broken veld	<u>Carissa</u>
7. Pakhuispas	Low fynbos	<u>Protea glabra</u>
8. Uitkomsberge	Fynbos	<u>Protea</u> , <u>Euclea</u>
9. Keurbos, Clanwilliam	Karoid broken veld	<u>Rhus incisa</u>
10. Pakhuispas	Tall fynbos	<u>Protea nitida</u>
11. Algeria	Kloof woodland	<u>Brabejum</u>
12. Grootrivierpas	Succulent karoo	<u>Cotyledon</u> , <u>Ruschia</u>
13. Suurfontein	Succulent karoo	<u>Euphorbia</u> , <u>Hoodia</u>
14. Brakfonteinspruit	Low karoo	<u>Eriocaulus</u>
OUTENIQUA-SWARTBERG AREA		
1. Hartenbos	Coastal renosterveld	<u>Elytropappus</u>
2. Hartenbos	Tall renosterveld	<u>Elytropappus</u>
3. Hartenbos	Valley bushveld	<u>Aloe ferox</u>
4. Bonnievale	Fynbos	<u>Protea repens</u>
5. Ruitersbos	Tall fynbos	<u>Protea coronata</u>
6. Robinson Pass	Kloof woodland	<u>Virgilia</u> , <u>Alsophila</u>
7. Knysna	Knysna forest	<u>Podocarpus</u> , <u>Olea</u>
8. Kliprivier	Low mt. renosterveld	<u>Elytropappus</u>
9. Kliprivier	Mt. renosterveld	<u>Elytropappus</u>
10. Kliprivier	Spekboom-renosterveld	<u>Elytropappus</u>
11. Oudtshoorn	Spekboomveld	<u>Portulacaria</u>
12. Alwynkoppe	Mt. thorn scrub	<u>Cussonia</u> , <u>Maytenus</u> , <u>Aloe</u>
13. Swartbergpas	Mt. renosterveld	<u>Elytropappus</u>
14. Swartbergpas	Open fynbos	<u>Protea nitida</u>
15. Swartbergpas	Dense fynbos	<u>Protea eximia</u> , <u>P. punctata</u>
16. Scholtzkloof	Bushveld	<u>Acacia karroo</u>
17. Prince Albert	Karoid broken veld	

^a Habitat variables 1-6 are described in the text. ^b PCI, PCII refer to derived from all 44 sites listed.

species' presence, asterisks its absence.

Site area (ha)	Habitat variables ^a						PCI ^b	PCII
	1	2	3	4	5	6		
2.41	-0.013	0.072	-0.097	0.903	-0.014	1.500	-0.73	0.93
1.20	0.530	0.076	-0.071	1.146	0.046	1.400	-0.57	0.80
3.33	0.267	0.140	0.176	1.380	0.194	0.700	-0.49	0.11
2.58	0.322	0.146	0.176	1.223	0.263	1.300	-0.42	0.46
1.67	0.532	0.152	0.477	1.519	0.350	0.700	-0.24	-0.10
2.52	0.596	0.260	0.415	1.322	0.451	1.400	-0.17	0.27
1.76	0.740	0.462	0.544	1.146	0.646	1.500	-0.16	0.07
1.71	0.769	0.461	0.602	1.491	0.516	1.130	0.05	-0.07
2.22	0.892	0.491	0.634	1.447	0.616	1.161	0.04	-0.18
1.86	1.037	0.322	0.653	1.724	0.602	0.778	0.11	-0.42
4.59	1.131	0.649	0.681	1.649	0.686	0.699	0.16	-0.65
0.74	1.556	1.212	1.380	1.954	0.796	1.16	1.27	-0.44
2.81	1.888	1.305	1.602	1.681	1.123	1.600	1.12	-0.78
5.55	0.462	0.699	0.243	0.991	0.466	1.255	-0.49	0.11
3.76	0.580	1.000	0.431	1.004	0.578	1.362	-0.06	0.46
11.15	0.653	0.845	0.358	0.869	0.751	0.954	-0.38	0.07
3.33	0.785	1.041	0.439	1.265	0.621	0.892	0.06	-0.02
5.57	0.799	1.041	0.550	1.030	0.776	1.130	0.06	0.01
7.50	0.839	1.415	0.078	0.978	0.858	1.146	0.29	-0.17
4.18	0.949	0.204	0.628	1.193	0.795	0.954	-0.12	-0.03
5.02	0.962	1.301	0.708	1.196	0.806	1.161	0.43	-0.17
5.83	0.964	0.415	0.342	0.820	1.176	0.845	-0.58	-0.39
2.97	1.143	1.255	0.748	1.438	0.795	0.778	0.55	-0.53
1.46	1.362	1.996	1.227	1.575	0.865	1.516	1.56	-0.44
8.33	0.580	0.955	0.414	0.806	0.720	1.146	-0.31	0.23
30.10	0.415	0.845	0.146	0.462	0.898	1.049	-0.90	0.21
15.06	0.477	0.955	0.267	0.724	0.659	1.301	-0.44	0.46
3.54	0.580	0.903	0.420	1.199	0.484	1.415	0.05	0.59
3.63	0.690	0.954	0.435	1.140	0.605	1.255	0.02	0.31
4.77	0.940	1.362	0.782	1.305	0.720	1.250	0.61	-0.06
4.77	0.964	1.322	0.832	1.300	0.742	1.301	0.64	-0.05
3.47	1.152	1.-14	0.591	1.373	0.839	0.699	0.32	-0.57
1.20	1.757	2.643	0.086	0.429	0.395	-0.317	11.77	-1.91
20.00	2.455	3.625	0.108	0.958	0.352	-0.352	2.70	-2.47
3.23	0.431	0.699	0.230	0.724	0.595	1.130	-0.63	0.48
2.22	0.633	1.000	0.519	1.233	0.513	1.491	0.22	0.55
4.81	0.622	1.000	0.435	1.117	0.557	1.274	0.01	0.39
3.70	0.832	1.114	0.431	0.839	0.992	0.699	-0.30	-0.45
4.17	0.875	1.146	0.628	0.959	0.912	1.097	0.08	-0.18
6.02	0.699	1.114	0.571	1.173	0.596	1.498	0.27	0.43
3.63	0.875	1.000	0.556	1.283	0.682	1.000	0.20	-0.05
2.13	0.881	1.146	0.720	1.356	0.650	1.295	0.51	0.12
6.25	1.068	1.255	0.415	0.924	1.156	0.556	-0.18	-0.84
29.50	0.580	0.955	-0.208	0.279	2.079	0.556	-1.59	-0.98

the first two principal components of the habitat variables 1-6,

Appendix C. Bird census results from sites in the Cape Town-Jonkershoek Area. Data are densities as pairs ha⁻¹ or equivalent for gregarious species (see text). Asterisks indicate species' absence.

SITE NUMBER: H:	1 -0.09	2 -0.03	3 0.20	4 0.25	5 0.43	6 0.53	7 0.72	8 0.74	9 0.85	10 0.93	11 0.97	12 1.56	13 1.83
BIRD SPECIES													
1. <i>Calandrella cinerea</i>	0.30	**	0.30										
2. <i>Galerida magnirostris</i>	0.35	0.35	0.30	0.40									
3. <i>Anthus novaeseelandiae</i>	0.62	**	0.12										
4. <i>Cisticola textrix</i>	1.49	1.49	0.89	0.40	0.25								
5. <i>Macronyx capensis</i>	0.15	0.15	**	0.15	**	0.30							
6. <i>Anthus leucophrys</i>	0.84	0.25											
7. <i>Mirafra apiata</i>	0.32	**	0.77										
8. <i>Coturnix coturnix</i>			0.20	**									
9. <i>Telophorus zeylonus</i>			0.20	**									
10. <i>Cisticola subruficapilla</i>			0.40	0.60	1.59								
11. <i>Francolinus capensis</i>			0.30	0.40		0.27	0.60	0.45					
12. <i>Sphenoeacus afer</i>			0.60	**		0.27	1.17	1.81	1.34				
13. <i>Prinia maculosa</i>			0.60	1.59		2.55	2.63	1.12	1.07	0.47			
14. <i>Euplectes capensis</i>			0.12	0.79	0.57	*			0.22	0.27			
15. <i>Serinus flaviventris</i>			0.99	2.28	1.76								
16. <i>Erythropygia cornuta</i>			0.69	1.41	1.16								
17. <i>Numida meleagris</i>			0.20	0.57									
18. <i>Streptopelia senegalensis</i>			0.40	1.14									
19. <i>Emberiza capensis</i>			0.40	0.57	0.87								
20. <i>Cinnyris chalybeus</i>			0.40	0.57	1.17								
21. <i>Streptopelia capicola</i>			0.99	1.14	0.30	0.89	0.82	0.12	0.25	0.25			
22. <i>Sigelius silens</i>			0.20	**		0.45	0.40	0.12	0.67				
23. <i>Oena capensis</i>			0.27		0.87								
24. <i>Serinus canicollis</i>			0.27	**		0.89	1.07	0.37	0.97	0.89			
25. <i>Cossypha caffra</i>			0.27	1.17	1.12	0.40	0.77	1.56	1.00				
26. <i>Zosterops pallidus</i>			0.84	1.17	0.45	0.82	0.84	1.36	2.48				
27. <i>Saxicola torquata</i>					0.15								
28. <i>Parisoma subcaeruleum</i>					0.60								
29. <i>Serinus albogularis</i>					0.37								
30. <i>Pycnonotus capensis</i>					1.76	0.45	0.82	0.99					

31. <u><i>Francolinus africanus</i></u>	0.60	**	0.82	0.37	0.12	
32. <u><i>Onychognathus morio</i></u>	0.60	0.25	1.07	0.25	**	0.12
33. <u><i>Apalis thoracica</i></u>	0.60	0.12	**	0.47	1.36	
34. <u><i>Corvus albicollis</i></u>	1.12	0.10	0.12	0.07		
35. <u><i>Promerops cafer</i></u>	1.59	0.82		1.44		
36. <u><i>Nectarinia violacea</i></u>	0.89	0.82	1.09			
37. <u><i>Serinus leucopterus</i></u>	0.45	0.82	0.37			
38. <u><i>Laniarius ferrugineus</i></u>	0.22	0.25	0.67	1.56	0.35	
39. <u><i>Batis capensis</i></u>	0.22	**	0.67	2.70	1.41	
40. <u><i>Monticola rupestris</i></u>	0.82	0.20				
41. <u><i>Nectarinia famosa</i></u>	1.61	0.15	0.67			
42. <u><i>Cisticola fulvicapilla</i></u>	0.27	0.15				
43. <u><i>Serinus sulphuratus</i></u>	1.07	0.20				
44. <u><i>Mesopicos griseocephalus</i></u>	0.12	0.20	**	0.12		
45. <u><i>Streptopelia semitorquata</i></u>	0.12	0.27	0.17			
46. <u><i>Bradypterus victorini</i></u>	0.25					
47. <u><i>Turdus olivaceus</i></u>		0.97	0.94			
48. <u><i>Tersiphone viridis</i></u>		0.45	0.89			
49. <u><i>Andropadus importunus</i></u>			1.41			
50. <u><i>Muscicapa adusta</i></u>			1.07			
51. <u><i>Columba arquatrix</i></u>				0.35		
52. <u><i>Bradypterus sylvaticus</i></u>				0.50		
53. <u><i>Aplocephala larvata</i></u>				0.25		
TOTAL BIRD SPECIES:						
TOTAL BIRD DENSITY (pairs ha ⁻¹):	5	5	6	16	24	13
	2.91	3.15	1.86	2.52	2.47	17
				16.98	13.28	12.91
				21.20	15.74	12.30
				10.47		

Appendix D. Bird census results from sites in the Clanwilliam-Cederberg area. Asterisks indicate species' absence.

	TOTAL BIRD SPECIES:	TOTAL BIRD DENSITY (pairs ha ⁻¹):
B1. <i>Melaenornis infuscatus</i>	0.05	
Creatophora cinerea	0.12	
Myrmecocichla formicivora	0.07	
Eremomela icteropygialis	0.10	0.06
<i>Corvus albus</i>	0.02	
Sylvietta rufescens	0.05	
<i>Cercomela schlegelii</i>	0.07	
Pachycephala capensis	0.15	
<i>Parus afer</i>	0.05	
<i>Colius colius</i>	0.10	
Parisoma subcaeruleum	0.37	
<i>Ploceus capensis</i>	0.15	
<i>Sigelus silens</i>	0.17	
<i>Serinus sulphuratus</i>	0.25	
<i>Columba guinea</i>	0.30	
Onychognathus morio	0.17	
<i>Cossypha cafra</i>	0.12	
<i>Zosterops pallidus</i>	0.12	
<i>Bradypterus victorini</i>	0.50	
<i>Nectarinia violacea</i>	0.47	
Promerops cafer	0.12	
<i>Sphenoeacus afer</i>	0.69	
<i>Oenanthe monticola</i>	0.67	
<i>Numida meleagris</i>	0.07	
<i>Batis pririt</i>	0.12	
<i>Laniarius ferrugineus</i>	0.25	
<i>Turdus olivaceus</i>	0.69	
<i>Eremomela gregalis</i>	0.07	
Unidentified lark	0.17	
<i>Estrilda astrild</i>	0.03	
Pterocles namaqua	0.02	0.05
<i>Galerida magnirostris</i>	0.02	
<i>Serinus alario</i>	0.07	

Appendix E. Bird census results from sites in the Outeniqua-Swartberg area. Asterisks indicate species' absence.

BIRD SPECIES	Site number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Habitat H:	0.51	0.61	0.89	0.90	1.19	1.65	1.97	0.15	0.62	0.66	0.95	1.03	0.79	0.89	1.04	1.31	0.52	
1. <i>Spreo bicolor</i>	0.12	0.12	**	**	**	**	**	0.15	**	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.25	
2. <i>Cisticola subruficapilla</i>	1.04	0.77	**	**	**	**	**	0.62	0.89	0.62	1.02	0.20	0.57	0.50	**	**	0.25	
3. <i>Serinus Flaviventris</i>	0.42	0.47	0.20	**	**	**	**	0.15	**	0.12	0.40	0.17	0.12	0.17	0.17	0.17	0.47	
4. <i>Erythropygia cornifrons</i>	0.62	0.94	0.37	**	**	**	**	0.89	0.52	0.69	0.42	0.15	**	**	**	**	0.47	
5. <i>Emberiza capensis</i>	0.50	0.69	0.20	0.27	**	**	**	0.69	0.42	0.69	0.72	0.07	0.12	0.12	0.12	0.12	0.52	
6. <i>Sphenoeacus afer</i>	0.35	0.69	**	0.50	0.64	**	**	**	**	**	**	**	0.32	0.74	0.74	0.84	0.84	
7. <i>Prinia maculosa</i>	1.26	1.44	0.94	0.74	1.14	**	**	0.89	0.42	0.92	0.47	0.50	0.27	0.84	0.84	0.84	0.57	
8. <i>Streptopelia capicola</i>	0.07	0.42	0.32	0.30	0.47	0.25	**	0.22	0.20	0.40	0.37	0.17	0.42	0.35	0.35	0.35	0.15	
9. <i>Nectarinia famosa</i>	0.42	0.22	0.32	0.15	0.30	0.74	**	0.32	0.32	0.10	0.25	0.22	0.47	**	0.45	**	0.40	
10. <i>Pycnonotus capensis</i>	0.26	**	0.20	0.30	**	0.50	**	0.12	**	0.22	0.47	**	0.45	**	0.45	**	0.40	
11. <i>Nectarinia chalybea</i>	0.07	0.22	0.42	**	0.35	0.62	0.22	**	**	0.37	0.55	0.47	0.07	0.27	0.27	0.27	0.25	
12. <i>Apalis thoracica</i>	0.27	0.87	1.14	0.52	**	0.77	0.45	**	**	0.37	0.64	0.07	0.50	0.47	0.47	0.47	0.25	
13. <i>Andropadus importunus</i>	0.02	0.27	1.04	0.30	**	0.37	1.24	**	0.32	0.45	**	**	**	**	**	**	0.15	
14. <i>Oena capensis</i>	0.22	**	**	**	**	**	**	**	0.32	0.45	**	**	**	**	**	**	0.15	
15. <i>Emberiza impetuani</i>	0.69																	
16. <i>Mirafra apiata</i>	0.12	**	**	**	**	**	**	**	**	**	0.30	**	**	0.07	0.07	0.07	0.07	
17. <i>Lanius collaris</i>	0.42	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	0.02	
18. <i>Telophorus zeylonus</i>	0.27	0.17	**	**	**	**	**	0.22	0.45	0.32	0.55	0.25	0.07	**	**	**	0.32	
19. <i>Streptopelia senegalensis</i>	0.42	0.32	**	**	**	**	**	**	**	0.60	0.42	0.05	**	**	**	**	0.02	
20. <i>Colius striatus</i>	0.35	0.62	**	**	**	**	**	**	0.20	0.35	**	0.20	0.35	**	0.27	**	0.57	
21. <i>Tchagra tchagra</i>	0.12	0.20	**	**	**	**	**	**	**	0.25	**	**	0.12	0.40	0.05	1.04	0.42	
22. <i>Cisticola fulvicapilla</i>	0.27	0.62	0.72	0.30	**	**	**	**	**	**	**	**	**	0.45	0.45	0.45	0.27	
23. <i>Euplectes capensis</i>	0.12	**	**	0.52	**	**	**	**	**	**	**	**	0.25	0.12	0.15	0.15	0.15	
24. <i>Serinus sulphuratus</i>	0.22	**	**	0.15	**	**	**	**	**	0.12	0.72	0.50	0.20	**	**	**	0.57	
25. <i>Cossypha caffra</i>	0.27	0.74	0.60	0.69	0.99	0.22	**	**	**	**	0.15	0.12	0.55	0.79	0.15			
26. <i>Passer melanurus</i>	0.37	*	**	**	**	**	**	**	**	**	0.10	0.10	**	**	**	**	0.15	
27. <i>Signelus sibens</i>	0.37	*	**	**	0.52	**	**	**	**	**	0.22	0.25	0.25	0.45	0.45	0.45	0.27	
28. <i>Numida meleagris</i>	0.12	*	**	**	**	**	**	**	**	**	0.25	0.12	0.15	0.15	0.15	0.15	0.15	
29. <i>Parisoma subcaeruleum</i>	0.42	*	**	**	**	**	**	**	0.12	0.72	0.50	0.20	**	**	**	**	0.57	
30. <i>Streptopelia semitorquata</i>	0.12	0.20	0.15	0.25														
31. <i>Laniarius ferrugineus</i>	0.42	0.42	0.35	0.87	0.27	**	**	**	**	**	0.10	0.10	**	**	**	0.27	0.27	
32. <i>Zosterops pallidus</i>	0.62	0.79	0.69	1.24	1.36	**	**	**	**	**	0.47	0.07	0.55	1.07	1.07			
33. <i>Francoolinus capensis</i>	0.20	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	0.20	
34. <i>Promerops cafer</i>	0.20	0.87	**	**	**	**	**	**	**	**	**	**	**	0.82	1.07			
35. <i>Nectarinia violacea</i>	0.52	0.77	**	**	**	**	**	**	**	**	**	**	**	0.77	1.26			

36. <i>Bradypterus victorinii</i>	0.42	0.69	**	**	**	**	**	0.77	0.84
37. <i>Serinus canicollis</i>	0.10	0.42	0.62	**	**	**	**	0.45	0.74
38. <i>Dicrurus adsimilis</i>	0.20	0.07	0.25	0.07	**	**	0.10		
39. <i>Batis capensis</i>	0.60	0.55	1.98	0.50	**	**	**	**	0.12
40. <i>Serinus totta</i>	0.30				**	0.12	**	**	
41. <i>Serinus gularis</i>	0.30								
42. <i>Serinus scotops</i>	0.47	0.74	0.07						
43. <i>Muscicapa adusta</i>	0.15	0.50	0.27						
44. <i>Onychognathus morio</i>	0.25	0.02	**						
45. <i>Turdus olivaceus</i>	0.62	0.03							
46. <i>Terpsiphone viridis</i>	0.45	0.42							
47. <i>Tauraco corythaix</i>			0.20						
48. <i>Camaroptera brachyura</i>			1.46						
49. <i>Seicercus ruficapilla</i>			0.94						
50. <i>Nectarinia afra</i>			0.57						
51. <i>Cossypha dichroa</i>			0.45						
52. <i>Oriolus larvatus</i>			0.40						
53. <i>Dryoscopus cubla</i>			0.30						
54. <i>Coracina caesia</i>			0.30						
55. <i>Phyllastrephus terrestris</i>			0.27						
56. <i>Apaloderma narina</i>			0.27						
57. <i>Mesopicos griseoccephalus</i>			0.22						
58. <i>Columba arquatrix</i>			0.20						
59. <i>Aplocephala larvata</i>			0.17						
60. <i>Sarcophura elegans</i>			0.11						
61. <i>Telephorus olivaceus</i>			0.05						
62. <i>Dendropicos fuscescens</i>			0.05						
63. <i>Phoeniculus purpureus</i>			0.12						
64. <i>Campephaga flava</i>			0.05						
65. <i>Serinus albogularis</i>									
66. <i>Stenostira scita</i>									
67. <i>Certhilauda albescens</i>			0.94	**	0.52				
68. <i>Eupodotis afra</i>			0.07	**	0.17	**	0.05		
69. <i>Sylvietta rufescens</i>					0.20	0.12			
70. <i>Pterocles namaqua</i>			0.32	**	0.10	**	**	**	0.02

Appendix E (continued)

BIRD SPECIES	Site number: Habitat H:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
71. <i>Corvus capensis</i>																		
72. <i>Malcorus pectoralis</i>																		
73. <i>Cercomela familiaris</i>																		
74. <i>Cercomela schlegelii</i>																		
75. <i>Estrilda astrild</i>																		
76. <i>Anthus similis</i>																		
77. <i>Monticola rupestris</i>																		
78. <i>Saxicola torquata</i>																		
79. <i>Serinus leucopterus</i>																		
80. <i>Colius colius</i>																		
81. <i>Eremomela gregalis</i>																		
82. <i>Certhilauda curvirostris</i>																		
83. <i>Hippolais icterina</i>																		
TOTAL BIRD SPECIES:		13	24	23	20	22	18	31	11	11	21	26	15	23	14	15	7	
TOTAL BIRD DENSITY (pairs ha ⁻¹)	5.42	10.61	10.26	8.05	10.34	12.01	11.27	4.20	6.06	6.51	10.12	7.51	2.47	10.35	9.90	4.17	0.45	