The evolution and biogeography of seed dispersal in southern African trees

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INTRODUCTION

Many quantified biogeographical analyses have concentrated on describing patterns, while the processes that may influence the nature of these patterns are rarely considered. It is often felt that these processes are not really "geographical" but are "biological". In this thesis an attempt is made to investigate the biogeography and evolution of the southern African angiosperm tree flora in terms of seed dispersal processes.

The biology of seed dispersal is fairly complex, with much scope for the advancement of new hypotheses and testing of plant/environment and plant/animal relationships (McKey 1975). Biologists have generally reviewed all reproductive processes (plant and animal) in terms of a dichotomous strategy (Horn 1978). This strategy predicts that an organism will either opt for producing a large number of propagules each of which possess an individually low parental investment and a low probability of achieving reproductive maturity (an r-selected strategy), or to produce a small number of propagules, each with an individually large parental investment and a high relative probability of achieving reproductive maturity (a K-selected strategy).

In southern Africa most tree species appear to possess fruit types that are one of five morphological forms (berry, drupe, pod, capsule and nut) and may be assessed in terms of r- and K-selection. Further each fruit type may possess more than one dispersal mechanism.

The following is a synopsis of fruit type/dispersal mechanisms based on hypotheses of McKey (1975) and Van der Pijl (1969).

The berry is a fleshy fruit derived from a compound ovary, with many seeds embedded in the pericarp. This type of fruit is generally considered to have evolved with vertebrate dispersal agents. The fleshy pericarp provides food for a potential dispersal agent, while the agent provides the plant with translocation of its propagules. The large number of seeds contained within a berry fruit are suggestive of an r-selected reproductive strategy (McKey 1975).

The drupe is also a fleshy fruit but is derived from a single carpel, and is usually single-seeded. The single seed is consequently larger and may represent a K-selected reproductive strategy (McKey 1975).

The pod is a non-fleshy fruit derived from a single ovary composed of one carpel. At maturity the dry pericarp usually splits along both sutures and the seeds are thus released. Pods may be eaten and dispersed by large ungulates, although a high mortality usually occurs and consequently an r-selected reproductive strategy is anticipated. Seeds may also be autochorous (self-dispersed) or possess arils which are functionally analogous to a fleshy drupe. Plants possessing an arillate fruit have been considered to be limited to primitive families (Corner 1949).

Capsules are also dry fruits and the seeds contained within may be "tufted", "winged" or very small for wind facilitated dispersal. Alternately seeds may be sticky, arillate or surrounded by an edible pulp and consequently dispersed by birds or mammals.

Nuts are hard-shelled fruits usually possessing a single seed. They may have "winged" or "tufted" modifications for wind dispersal. Nuts without these appendages may be stored by birds and mammals in the form of nut caches and if unreclaimed dispersal may result (Snow 1971).

Theoretical discussions have been advanced on the evolutionary relationship existing between plants possessing fleshy or arillate fruits and avian seed dispersers. Theories of McKey (1975) and Howe & Estabrook (1977) predict that a small seeded plant species will attract a variety of opportunist avian frugivores with fruits of an individually low nutritional quality, whereas large-seeded species attract specialist frugivores with smaller displays of highly nutritious fruits. Some small seeds (those usually contained within capsules) may possess very small aril-like structures termed elaisosomes which are almost exclusively dispersed or stored by ants (Berg 1975).

AIMS

This thesis specifically addresses the following five aims :-

1. To identify fruit characteristics (type, size and colour) of southern African trees that may possibly have evolved for dispersal by birds and mammals.

2. To describe the biogeographical patterns of southern African trees which possess each of the five fruit forms (drupe, berry, pod, capsule or nut) and three dispersal mechanisms (bird, mammal or wind).

3. To relate the evolution of fruit characteristics (1st aim) and

the biogeographical patterns of fruit types (2nd aim) with a suite of environmental variables.

4. To describe the biogeographical patterns of the "primitive" aril-bearing tree flora, and to evaluate these results in terms of a possible evolution for the entire African angiosperm flora.

5. To describe the biogeographical patterns of the southern African frugivorous avifauna and to relate these results with the number, size and seasonal availability of fleshy fruits (on a species criteria).

This thesis consists of five published or submitted papers (parts 1-5) which relate to each of the above five aims. In each part the data sources, methods and references are discussed separately. This represents the first attempt at synthesising biogeographical and evolutionary aspects of angiosperm biology in terms of a quantified holistic methodology, and consequently these results should be considered as representing quantified hypotheses.

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PART 1

INTER-RELATIONSHIPS BETWEEN TYPE, SIZE AND COLOUR OF FRUITS AND DISPERSAL IN SOUTHERN AFRICAN TREES

ABSTRACT

The indigenous angiosperm tree flora (1 340 species) of southern Africa was analysed for type, size and colour of fruits and class of biotic dispersal agent (consumer). Species producing fleshy (drupes and berries) and dry (pods, capsules and nuts) fruits account for 52% and 47%, respectively, of the flora. The flora contains about 2,5 times as many berry-producing as drupe-producing species. Based on a log-linear model, fruit type, consumer and fruit size are dependent statistically on each other, whereas fruit colour depends on both fruit size and consumer type acting independently of each other. Drupes and berries are consumed by birds and mammals, with berries being favoured by both birds and mammals. At least 23% (307 species) of the flora apparently depends predominantly on birds for seed dispersal. Drupes and berries favoured by birds tend to be small and brightly coloured (red or black), whereas those eaten mainly by mammals tend to be large and dull (yellow or green). Relatively few fleshy fruits are brown. Pods, capsules and nuts tend to be brown or green. Birds apparently tend to avoid eating green fruits. The notion that green colouration has evolved to enhance crypsis and/or to signal unpalatability in unripe fruit to reduce premature exploitation is questioned. Green as a cryptic colour is incompatible with the demonstrated mammalian selection of this colour, while to function aposematically a stronger contrast colour may be required.

INTRODUCTION

Plant species which rely on animals for seed dispersal produce fruits whose characteristics vary in relation to the type of animal agent involved (Snow 1971). Amongst a host of fruit characteristics, fruit type and seed size (McKey 1975; Stiles 1980) and fruit colour (Turcek 1963) have been isolated for special study. This part reports quantitative information on the inter-relationships between fruit type, size and colour in the indigenous angiosperm tree flora of southern Africa in order to make a preliminary assessment of the flora's dependence on birds as seed dispersers. Aspects of the evolution of fruit characteristics which facilitate avian-based dispersal of seeds are also discussed.

METHODS

The fruits of 1 340 species of trees were classified according to type (drupe, berry, pod, capsule or nut), colour when ripe (white, red, orange, yellow, green, brown, and blue/black), and size (length in mm), using information taken from Palmer & Pitman (1972, 1973), Van Wyk (1972, 1974), Palmer (1977) and Coates Palgrave (1977). This information, together with data in Phillips (1927, 1931), Chapin (1932-1954), White (1962), Liversidge (1965), Huntley (1965), Skead (1965) and Oatley (1969), was used in the following categories: (a) species whose fruits are known to be eaten frequently by birds (variable BIRD); (b) species congeneric with those in the preceding allocation and whose fruits apparently are palatable to birds and, thus, are likely to be eaten at least occasionally by birds (BIRD 2); (c) species whose fruits are known to be eaten by mammals (MAMMAL); and, (d) all other tree species

(OTHER).

Chi-square tests were used to identify relationships between fruit type and classes of consumers, fruit type and colour, and consumer class and colour. The null hypotheses were that fruit type and consumer, fruit type and colour, and consumer and colour are independent of one another ($\underline{P} < 0{,}05$). A computer program (BMDP P2F) was used to isolate sequentially larger contributions (i.e. cells) to the 'χ^2', until the remaining part of the contingency table showed no row-column effects (Fienberg 1972; Brown 1974, 1976a). A new table of expected values was calculated at each step.

A Kruskal-Wallis one-way analysis of variance (BMDP 2PS) was used to test for fruit size and fruit type variation amongst consumer and colour classes, with the null hypothesis that fruit size amongst the consumer classes could be the result of sampling from the same population for each of the fruit and colour classes ($\underline{P} < 0{,}05$). Conventional analysis of variance necessitates data to be distributed normally with a small variance ($\underline{s}^2$). Although a gamma distribution of fruit sizes could be normalized (Manly 1976), a high variance persisted and, therefore, distribution free tests were applied.

The results of all these tests were used to 'summarize' the data and produce a simplified four-way table of relationships between colour (C), size (S), consumer (E), and fruit type (F). With such multidimensional tables, it is conventionally necessary to proceed with a frequency analysis of the marginal totals (Kendall 1980), which has led investigators to suggest the nesting of hypotheses (Goodman 1969). Since there may be, however, a large number of hypotheses to be considered, it is necessary to see whether the hypothesis of interest can be parameterized (Kendall 1980; Fienberg 1970, 1977). If the probability of occurrence in a cell is regarded as multiplicative, it is possible to write a four-way classification of inter-relationships of colour (C), size (S), fruit consumed by biotic agents (E) and fruit type (F)

$$\begin{aligned} \mathrm{Log}_e\, F_{ijkl} = \theta &+ \lambda_i^{C} + \lambda_j^{S} + \lambda_k^{E} + \lambda_l^{F} \\ &+ \lambda_{ij}^{CS} + \lambda_{ik}^{CE} + \lambda_{jk}^{SE} + \lambda_{jl}^{SF} + \lambda_{kl}^{EF} + \lambda_{il}^{CF} \\ &+ \lambda_{ijk}^{CSE} + \lambda_{ijl}^{CSF} + \lambda_{jkl}^{SEF} + \lambda_{ikl}^{CEF} \\ &+ \lambda_{ijkl}^{CSEF} \end{aligned}$$

where the summation of any ' λ ' (effect) over any suffix is zero. If the suffix i refers to the C classification, etc., the term λ_i^C will represent the contribution of C to the i th row of the table. This is, as in an analysis of variance model, a log-linear hierarchical model. To fit the model a maximum likelihood estimate ($\underline{G}^2$) is used (see Appendix 1). The word 'effect' (λ) is used in the statistical sense, and it in no way establishes the positive existence of causal relationships among the variables. Indeed, the data is modelled on the assumption of causality to see how well any model fits the observed data. The smaller the $\underline{G}^2$ value, the better the fit of the model. The most parsimonious model that adequately explains the variation in the data (Williams 1976b) is fitted, using the BMDP 3F computer program (Brown 1976b).

Fruit type and consumer

Species producing fleshy fruits account for 52% of the indigenous tree flora, whereas 47% of the species possess dry fruits (pods, capsules and nuts), of which 11% contain arillate seeds. Further, at least 23% of the tree flora would seem to rely on birds for seed dispersal. The null hypothesis of independence between fruit type and consumer is rejected; variable OTHER being an 'extreme contribution' to the overall significance of the χ^2 value (Tables 1 & 2). Most species bearing pods, capsules and nuts occur in the group OTHER; these species being mainly wind dispersed (anemochorous). Berries, in both BIRD and MAMMAL categories, and drupes, in the BIRD2 category, exceed expected frequencies, reflecting an apparent selection for species with fleshy fruits by these animals. A re-analysis of these data, with OTHER removed entirely, indicates that although berries have higher than expected frequencies for MAMMAL and BIRD categories, only the higher than expected frequency for drupes in BIRD2 was isolated through the sequential cell removal technique. This suggests that fruit types for BIRD2 differ markedly from those in BIRD and MAMMAL, and may explain why the fruits of the BIRD2 species have not been observed to be eaten frequently.

Fruit type and colour

The null hypothesis of independence between colour and type of fruit is rejected (Tables 3 & 4). The brown berry and the brown drupe both have far higher expected than observed frequencies. The white capsule and the green capsule both have greater observed

Table 1. Contingency table of fruit types and consumer classes; values in parentheses are expected frequencies. 11 species could not be categorized for analysis

Consumer class	Fruit type					
	POD	CAPSULE	NUT	DRUPE	BERRY	Total
BIRD	0	23	0	79	178	280
	(36,66)	(66,37)	(29,29)	(47,61)	(99,44)	
BIRD2	1	16	0	31	19	67
	(8,77)	(15,88)	(7,16)	(11,39)	(23,80)	
MAMMAL	1	4	0	6	44	55
	(7,20)	(13,04)	(5,88)	(9,35)	(19,53)	
OTHER	172	272	142	110	231	927
	(121,37)	(219,72)	(99,05)	(157,64)	(329,23)	
Total	174	315	142	226	472	1329

Table 2. Summary of the steps for sequentially removing cells and isolating sources of significance in Table 1. Step 0 indicates the overall chi-square (χ^2) of the table, and further steps summarize the significance of the table with the select removal of individual cells that contribute most to the observed value. The last step indicates the stage where there are no row-column relationships

Step	Row	Column	χ^2	d.f.
0	n/a	n/a	371,63***	12
1	OTHER	POD	272,77***	11
2	OTHER	NUT	174,06***	10
3	OTHER	CAPSULE	46,46***	9
4	BIRD2	BERRY	15,14	8

* P < 0,05
** P < 0,01
*** P < 0,001

Table 3. Contingency table of fruit types and colour classes; the values in parentheses are expected frequencies. 184 species could not be categorized for analysis

Fruit colour	Fruit type					
	POD	CAPSULE	NUT	DRUPE	BERRY	Total
WHITE	4	24	7	7	6	48
	(6,93)	(9,47)	(4,57)	(8,68)	(18,36)	
RED	41	41	15	72	113	282
	(40,74)	(55,62)	(26,83)	(50,98)	(107,82)	
ORANGE	2	4	1	29	63	99
	(14,30)	(19,53)	(9,42)	(17,90)	(37,85)	
YELLOW	20	35	13	23	82	173
	(24,99)	(34,12)	(16,46)	(31,28)	(66,15)	
GREEN	6	35	11	13	37	102
	(14,74)	(20,12)	(9,71)	(18,44)	(39,00)	
BROWN	58	70	58	14	19	219
	(31,64)	(43,19)	(20,84)	(39,59)	(83,74)	
BLACK	36	19	5	51	122	233
	(33,66)	(45,95)	(22,17)	(42,13)	(89,09)	
Total	167	228	110	209	442	1156

Table 4. Summary of the steps for sequentially removing cells and isolating sources of significance in Table 3. Step 0 indicates the overall chi-square (χ^2) of the table, and further steps summarize the significance of the table with the select removal of individual cells that contribute most to the observed value. The last step indicates the stage where there are no row-column relationships

Step	Row	Column	χ^2	d.f.
0	n/a	n/a	346,07***	24
1	BROWN	BERRY	228,17***	23
2	BROWN	DRUPE	168,32***	22
3	WHITE	CAPSULE	132,33***	21
4	GREEN	CAPSULE	97,80***	20
5	BLACK	NUT	82,89***	19
6	YELLOW	CAPSULE	72,26***	18
7	ORANGE	POD	61,13***	17
8	ORANGE	NUT	49,71***	16
9	WHITE	NUT	41,67***	15
10	ORANGE	CAPSULE	32,68**	14
11	RED	NUT	25,39*	13
12	BLACK	CAPSULE	18,43	12

* $\underline{P} < 0,05$
** $\underline{P} < 0,01$
*** $\underline{P} < 0,001$

than expected frequencies, whereas orange has a relatively lower than expected frequency. No particular colour appears to predominate in pods, but the frequency of orange again is lower than expected. Frequencies of red, orange and black nuts are lower than expected, and there is a greater frequency of white nuts than expected.

Fruit colour and consumer

The null hypothesis of independence between consumer and colour of fruit is rejected (Tables 5 & 6). Brown in OTHER appears to be the most significant contribution to the contingency table, and probably reflects anemochorous elements. Orange has a far lower observed frequency than expected, and, therefore, is more characteristic of the other consumer groups. Green fruits appear not to be taken as frequently as expected in BIRD, whereas for MAMMAL there is a greater than expected frequency for species with green fruits. Birds select species which possess predominantly black fruits, and to a lesser extent orange and red, whereas red in mammals was lower than expected.

Fruit size and consumer

In the case of capsules and pods, the null hypothesis that BIRD, BIRD2, MAMMAL, and OTHER come from the same population (Table 7) is accepted. The drupe and berry size stratification among the consumer classes is pronounced. A comparison between species with drupes and those with berries indicates that for both types, mammals select fruits of similar size (Mann-Whitney $\underline{U}$ test = 154, $\underline{P} > 0{,}05$). Birds, however, select species with berries which are larger than drupes (Mann-Whitney $\underline{U}$ test = 2775, $\underline{P} < 0{,}05$). Drupes

Table 5. Contingency table of consumer classes and fruit colour; the values in parentheses are expected frequencies. 184 species could not be categorized for analysis

Fruit colour	Consumer class				
	BIRD	BIRD2	MAMMAL	OTHER	Total
WHITE	10	0	0	38	48
	(11,09)	(2,70)	(2,28)	(31,93)	
RED	72	17	6	187	282
	(65,13)	(15,86)	(13,42)	(187,59)	
ORANGE	39	9	9	42	99
	(22,87)	(5,57)	(4,71)	(65,86)	
YELLOW	44	10	17	102	173
	(39,96)	(9,73)	(8,23)	(115,08)	
GREEN	14	2	11	75	102
	(23,56)	(5,74)	(4,85)	(67,85)	
BROWN	14	3	5	197	219
	(50,58)	(12,31)	(10,42)	(145,68)	
BLACK	74	24	7	128	233
	(53,82)	(13,10)	(11,09)	(155,00)	
Total	267	65	55	769	1156

Table 6. Summary of the steps for sequentially removing cells and isolating sources of significance in Table 5. Step 0 indicates the overall chi-square (χ^2) of the table, and further steps summarize the significance of the table with the select removal of individual cells that contribute most to the observed value. The last step indicates the stage where there are no row-column relationships

Step	Row	Column	χ^2	d.f.
0	n/a	n/a	140,54***	18
1	BROWN	OTHER	67,41***	17
2	ORANGE	OTHER	53,49***	16
3	RED	MAMMAL	43,09***	15
4	GREEN	BIRD	34,41**	14
5	BLACK	BIRD2	26,40*	13
6	BLACK	BIRD	19,19	12

* $\underline{p} < 0,05$
** $\underline{p} < 0,01$
*** $\underline{p} < 0,001$

Table 7. Mean fruit length (mm) for fruit type among four consumer classes; the Kruskal-Wallis statistic (_H_) indicates significance of inter-consumer variation in fruit length among each of the fruit types

Variable	Statistic	POD	CAPSULE	NUT	DRUPE	BERRY
BIRD	Mean	10,00	58,65	0,00	7,75	13,21
	SD	0,00	205,74	0,00	7,30	7,68
	N	1	23	0	79	176
BIRD2	Mean	0,00	11,36	0,00	12,87	12,67
	SD	0,00	7,35	0,00	12,67	8,76
	N	0	14	0	30	19
MAMMAL	Mean	300,00	88,75	0,00	33,33	36,20
	SD	0,00	76,64	0,00	9,31	28,45
	N	1	4	0	6	44
OTHER	Mean	139,39	42,73	14,22	12,61	21,23
	SD	174,59	97,73	16,18	8,61	23,25
	N	172	230	125	108	227
All	_H_	n/a	6,76	n/a	55,36*	41,73*

* $P < 0,05$

and berries are also of similar size in the control category BIRD2 (Mann-Whitney *U* test = 227, *P* > 0,05).

Fruit size and colour

Fruit size differs in relation to colour in species bearing either berries, drupes or nuts (Table 8). For pods and capsules, the null hypothesis that samples of colour come from the same population is accepted. The species with the largest drupes tend to have yellow fruits. Green and orange drupes are also quite large, whereas the smallest are brown or black. Drupes are smaller than berries. The largest berries tend to be white or green. Brown and yellow berries are slightly smaller, and the smallest are black. The largest nuts are red and green. Orange pods tend to be relatively small.

Integration model

The inter-relationships between fruit type and consumer type, fruit size and colour are integrated in a multidimensional contingency table (Tables 9 & 10); only those two fruit types (drupe and berry) which appear to be dependent on animals for dispersal being included. A log-linear model of all these variables is fitted, which adequately explains the data with the fewest effects (λ). Marginal and partial association tests were used to 'screen' the data and to determine which effects, and combination of effects, should be incorporated in the model (Brown 1976c). These tests were highly significant for SE, FE and CS, while CE and SFE were also significant (Table 11). In testing four suites of effects, or models M1-M4, M1 is found to have a non-significant most parsimonious fit (Table 12) and, therefore,

Table 8. Mean fruit length (mm) for fruit type among seven colour classes; the Kruskal-Wallis statistic (H) indicates significance of inter-consumer variation in fruit length among each of the fruit types

Variable	Statistic	POD	CAPSULE	NUT	DRUPE	BERRY
WHITE	Mean	127,50	22,00	8,71	6,00	53,50
	SD	56,79	26,87	9,64	2,94	52,89
	N	4	24	7	7	6
RED	Mean	145,90	46,66	31,40	13,06	14,21
	SD	143,41	94,21	18,31	10,12	9,65
	N	41	38	15	71	112
ORANGE	Mean	72,50	13,25	25,00	10,48	19,94
	SD	67,18	7,89	0,00	9,90	21,82
	N	2	4	1	29	63
YELLOW	Mean	116,00	43,18	20,00	17,27	21,82
	SD	89,98	144,96	15,65	13,35	21,25
	N	20	34	13	23	82
GREEN	Mean	103,33	48,64	27,09	10,08	37,14
	SD	26,58	77,96	19,68	6,50	24,23
	N	6	33	11	13	37
BROWN	Mean	162,07	62,93	10,25	7,64	24,71
	SD	256,80	11,09	13,32	8,56	13,51
	N	58	69	57	14	17
BLACK	Mean	137,78	68,84	4,00	9,77	12,15
	SD	105,29	225,88	3,00	5,76	12,63
	N	36	19	3	51	120
All	$\underline{H}$	3,99	6,61	33,82*	22,84*	84,41*

* $\underline{P} < 0{,}05$

Table 9. Categories used in the four-dimensional contingency table for modelling the effects of consumer, fruit type, length (size) and fruit colour on each other

			Category number						
Variable	Symbol	Index	1	2	3	4	5	6	7
Colour	(C)	i	WHITE	RED	ORANGE	YELLOW	GREEN	BROWN	BLACK
Size	(S)	j	< 15	15-30	>30				
Fruit	(F)	k	DRUPE	BERRY					
Consumer	(E)	l	BIRD	BIRD2	MAMMAL				

Table 10. Four-dimensional contingency table of consumer, fruit type, length (size) and colour in relation to each other, and arranged in a hierarchy of effects

Consumer (E)	Fruit (F)	Size (S)	Colour (C)						
			1	2	3	4	5	6	7
BIRD	DRUPE	<15	4	24	12	7	5	10	10
		15-30	0	0	0	2	0	0	0
		>30	0	0	2	1	0	0	0
	BERRY	<15	1	36	19	20	2	3	55
		15-30	1	9	4	10	5	1	6
		>30	1	2	1	0	0	0	0
BIRD2	DRUPE	<15	0	3	4	0	0	1	15
		15-30	0	3	0	3	0	0	1
		>30	0	3	0	0	0	0	0
	BERRY	<15	0	7	3	0	0	0	0
		15-30	0	1	0	0	0	0	2
		>30	0	0	1	0	0	0	0
MAMMAL	DRUPE	<15	0	0	0	0	0	0	0
		15-30	0	2	1	0	0	0	0
		>30	0	0	0	2	1	0	0
	BERRY	<15	0	3	6	4	0	1	2
		15-30	0	1	1	6	0	0	3
		>30	0	0	1	5	7	2	1

Table 11. Tests of partial and marginal association for each subset of effects (Brown 1976c)

		Partial association[1]		Marginal association[2]	
Effect	d.f.	G²	probability	G²	probability
C	6	146,41	0,0000		
S	2	214,55	0,0000		
F	1	36,22	0,0000		
E	2	181,84	0,0000		
CS	12	38,36	0,0001	49,91	0,0000
CF	6	15,08	0,0197	12,26	0,0565
CE	12	22,27	0,0346	31,08	0,0019
SF	2	3,97	0,1373	3,21	0,2005
SE	4	52,70	0,0000	63,58	0,0000
FE	2	27,15	0,0000	23,66	0,0000
CSF	12	10,16	0,6017	11,35	0,4990
CSE	24	19,55	0,7220	18,77	0,7643
CFE	12	15,79	0,2011	14,30	0,2818
SFE	4	12,80	0,0123	9,71	0,0456
CSFE	24	13,46	0,9579		

[1] Partial association is calculated as the difference between the full order model and that which excludes only the subset of effects.

[2] Marginal association is calculated as the summation of the table over the unspecified indices and then the specified subset of effects are tested to be zero.

Table 12. The characteristics of four models derived from the results of partial and marginal association tests. M1 appears the most parsimonious model in explaining relationships between consumer, fruit type, length, and colour. However, tests of difference between this model and the other three models (M2-M4) indicate Model 4 to be the most suitable (see text)

Model		d.f.	G^2	probability	% variation
SE FE CS	M1	96	107,02	0,2078	56,17
SE FE CS CE	M2	84	87,73	0,3960	64,07
SFE CS	M3	90	93,58	0,3772	61,67
SFE CS CE	M4	78	74,29	0,5981	69,57

may be used to explain the variation in the data. The most significant difference in tests of fit between this and other models was found with M4, and this model appears to be the best fit for the data. The percentage of variation explained by M4 is 69.57%. The final log-linear model applied is

$$\begin{aligned}\mathrm{Log}_e\, F_{ijkl} &= \theta + \lambda_i^C + \lambda_j^S + \lambda_k^E + \lambda_l^F \\ &\quad + \lambda_{ij}^{CS} + \lambda_{ik}^{CE} + \lambda_{jk}^{SE} + \lambda_{jl}^{SF} + \lambda_{kl}^{EF} + \lambda_{jkl}^{SEF}\end{aligned}$$

Hence, in this model, fruit size (S) and consumer (E) and fruit type (F) are related and dependent on each other. Colour depends on fruit size and consumer but not on fruit type, whereas the influences of fruit size and consumer on colour are independent of each other.

DISCUSSION

Evolution of colour of fleshy fruit

The results indicate that species with drupes and berries tend to display particular fruit colours, and that the colours differ according to whether the fruits are eaten predominantly by mammals or birds. Species with yellow, orange and green fruits tend to be favoured by mammals, whereas birds favour black, and to a lesser extent, orange and red fruits. It is generally accepted that large fruits are mammal dispersed (Snow 1971) and, therefore, will have 'mammal colours'. Most mammals have monochrome vision, whereas primates and birds are equipped with colour vision (Hildebrand 1974). Fruit colour probably functions best as an attractant when contrasted against a differently coloured background. The combination of large size and white colour in certain fruits (Table 8) is probably an adaptation for attracting bats, as seed dispersers (van der Pijl 1969b).

The incidence of tree species producing white, orange, yellow or green fruits is much lower in Europe, where red and black fruits predominate for dispersal by birds (Turcek 1963), than in southern Africa. This difference presumably reflects a disproportionate influence of mammals, particularly the relative abundance of primates and fruit bats as seed-dispersers in southern Africa. In southern Africa, the relatively large size of yellow and orange drupes and berries conceivably enhances primate-based dispersal of seeds. Species with smaller, orange fruits might be dispersed mainly by birds.

The results also show that among species with fruits favoured by birds, orange fruits tend to be larger than red and black fruits, in that order. This might be a function of the foraging behaviour of birds of different sizes. Small birds might tend to search for fruits within the cover of trees, whereas large birds search for fruits while on the wing. This implies that fruits taken by large birds require to be more conspicuous, with regard to position in tree as well as colour and size.

Birds evidently are less likely to eat green fruits (Tables 5 & 6). Green may signal unpalatability (Corner 1949) or enhance crypsis (Snow 1971), thus providing some protection against premature exploitation and/or destruction by vertebrate predators. If a signal of unpalatability is assumed, it becomes debatable whether green provides the necessary visual impact to reinforce conditioned avoidance after birds have experienced the poisonous and/or distasteful nature of fruits of this colour. Unpalatability is advertized by high-contrast colour patterns (aposematic colouration) in many animal classes. It could be argued that the option of evolving high contrast colours in unripe fruit is closed to flowering plants, because evolution has favoured such colours as an attractant for avian frugivores through which effective dispersal of propagules can be achieved. The case against green as a cryptic colour generally is the demonstrated mammalian selection of green berries. If mammals, many of which have monochrome vision, are able to exploit preferentially such fruits, there seems little reason for birds not to do likewise. Thus, greenness, and the associated unpalatability of unripe fruits, could be a consequence of genetic pleiotropy (potential of a single gene to control more than one aspect of a phenotype), with no significant cryptic or advertizing function.

Evolution of colour of non-fleshy fruit

In general, birds and mammals select fleshy fruits ahead of capsules, pods and nuts (Tables 1 & 2). However, tree species with arillate seeds in capsules and pods rely on animals for dispersal, and are believed to represent an early stage in the evolution of zoochory (Corner 1949). Arillate seeds, having bright colours, tend to be dispersed by birds (Skutch 1980); those lacking bright colours are probably dispersed by ants (Berg 1975).

Green capsules occurred at greater than expected frequencies (Tables 3 & 4) and, depending on background and point of observation, may enhance crypsis and, hence, reduce losses due to consumption by browsing mammals. White capsules also occurred at greater than expected frequencies. Many white capsules possess a covering of fine white or transparent hairs which are good reflectors of light, and the fruits may therefore be fairly inconspicuous. The fact that species with orange capsules and pods tend to be very small (Table 8) might be related to a reduction in conspicuousness, providing that this colour is an inescapable consequence of pleiotropy.

Nuts are transported and stored by birds and mammals in cool temperate regions experiencing severe winters. Many such nuts are not reclaimed, and thus are dispersed effectively. The winters in southern Africa are probably too mild to promote the widespread evolution of such a system. Red, orange and black are poorly represented as colours for nuts; brown being most common (Tables 3 & 4). Since nuts tend to be spherical and of similar size to many bird-selected fleshy fruits (Tables 3 & 4), they could be susceptible to accidental removal for inspection by frugivores. Hence, selection favouring the evolution of a colour (brown) least characteristic of fleshy fruits might be expected. The species with the largest nuts have red and green fruits (Table 8), and generally are produced by anemochorous Combretum and Terminalia species. The selective advantage attending any colouration in anemochorous fruits would appear to be inconsequential, unless the colour enhances crypsis or functions aposematically. In the case of red nuts, the colour might be advantageous in promoting crypsis in an autumnal-coloured foliage background.

Aposematic colouration, with obligate fruit unpalatability, might have evolved with advantage in anemochorous fruits. Most of these, however, are brown, and apparently their main defence against predators is the production of very large numbers of propagules and the hard, woody pericarp enclosing the seed (Snow 1971). If the majority of anemochorous species are of more recent origin than those producing fleshy fruits, as van der Pijl (1969a) suggests, the adoption of high-contrast colours by the latter for attracting vertebrate dispersers, chiefly birds and primates, might have precluded aposematic colouration in anemochory.

Evolution of size of fruit

Size partitioning of zoochorous fruits is very pronounced, with mammals selecting berries approximately three times the size of those selected by birds (Table 7). This is perhaps surprising, since mammal or bird-based dispersal of a fruit should also depend on the relative softness or hardness of the pericarp. Large fruits having soft pericarps (e.g. some Ficus species) can be consumed (in pieces) by even small frugivores, promoting dispersal if the seeds are small. Alternatively, small fruits with hard pericarps (e.g. some Strychnos species) will not be consumed easily by birds. The most suitably sized fruits for ornithochory are red or black (Table 8), and both red drupes (the most common drupe colour) and black berries (the most common berry colour) are similar in size.

Evolution of type of fruit

Species producing fruits whose seeds are dispersed predominantly by birds or mammals have been classed as specialists (dependent on obligate frugivores) or opportunists (Morton 1973; McKey 1975; Howe & Estabrook 1977). Assuming that all drupes with their single seeds are fruits of specialists and all berries with their multitudes of seeds are fruits of opportunists, the southern African tree flora contains about two and a half times as many opportunist as specialist species. This might be related to the fact that, whereas drupes tend to supply dispersers with proteins and lipids, berries not only are larger (Table 7) but contain relatively more water which could be an important 'reward' for avian dispersers in semi-arid southern Africa. The indehiscent capsules of some species (e.g. Kigelia) are eaten by large animals (e.g. hippopotamus) which might disperse their seeds. Dehiscent capsules which contain arillate seeds are, however, generally an adaptation for biotic dispersal (Skutch 1980). Seeds contained in pods probably are dispersed by ungulates (Lamprey et al. 1974; van der Pijl 1969a), and within the southern African tree flora few species produce pods possessing seeds with well developed arils.

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PART 2

THE BIOGEOGRAPHY OF SEED DISPERSAL IN SOUTHERN AFRICAN TREES

ABSTRACT

Comparisons are made between the geographical distributions of southern African tree species possessing fruits which are either drupes, berries, pods, capsules or nuts and those which are dispersed by wind, avian or mammalian agents. For most fruit types, regions of similar species composition orientate in accord with both latitudinal and longitudinal belts, whereas patterns of proportional species richness (the percentage of a specified fruit type in the total tree flora) tend to form longitudinal belts. Autocorrelation coefficients tend to be low in diagonal directions (NE-SW and NW-SE), indicating a poor degree of spatial dependence for proportional species richness. These results are interpretated in relation to two environmental gradients, tropical-temperate and mesic-xeric as well as an opportunistic (r-selected) and specialist (K-selected) reproductive strategy gradient. The implications are discussed in terms of plant dispersal agents and contemporary coevolutionary theory.

The reproductive strategies and consequent dispersal of plant species should become less specialized as environments become less predictable in terms of their physical parameters. Thus, broad generalizations describing relationships between environment and predicted reproductive strategies have been advocated (Van der Pijl 1969a & b).

Rainforests are assumed to possess many fleshy non-dormant fruits (probably of drupe form) which germinate immediately and in the shade; the seedlings awaiting opportunities for growth. The seeds, therefore, require a large energy investment and represent a K-selected (specialist) reproductive strategy. In open or secondary vegetation fleshy fruits are likely to possess many seeds (viz berry form) in order to maximize efficient dispersal to the many vacant spaces present. Therefore, relatively less energy is required in each propagule, and an r-selected reproductive strategy is represented. Pod fruit forms may predominate in arid areas, because of their enhanced potential for dormancy. Species producing nuts (many of which are wind-dispersed) are considered to predominate in the temperate areas, whereas species producing capsules are unlikely to be confined to regional limits.

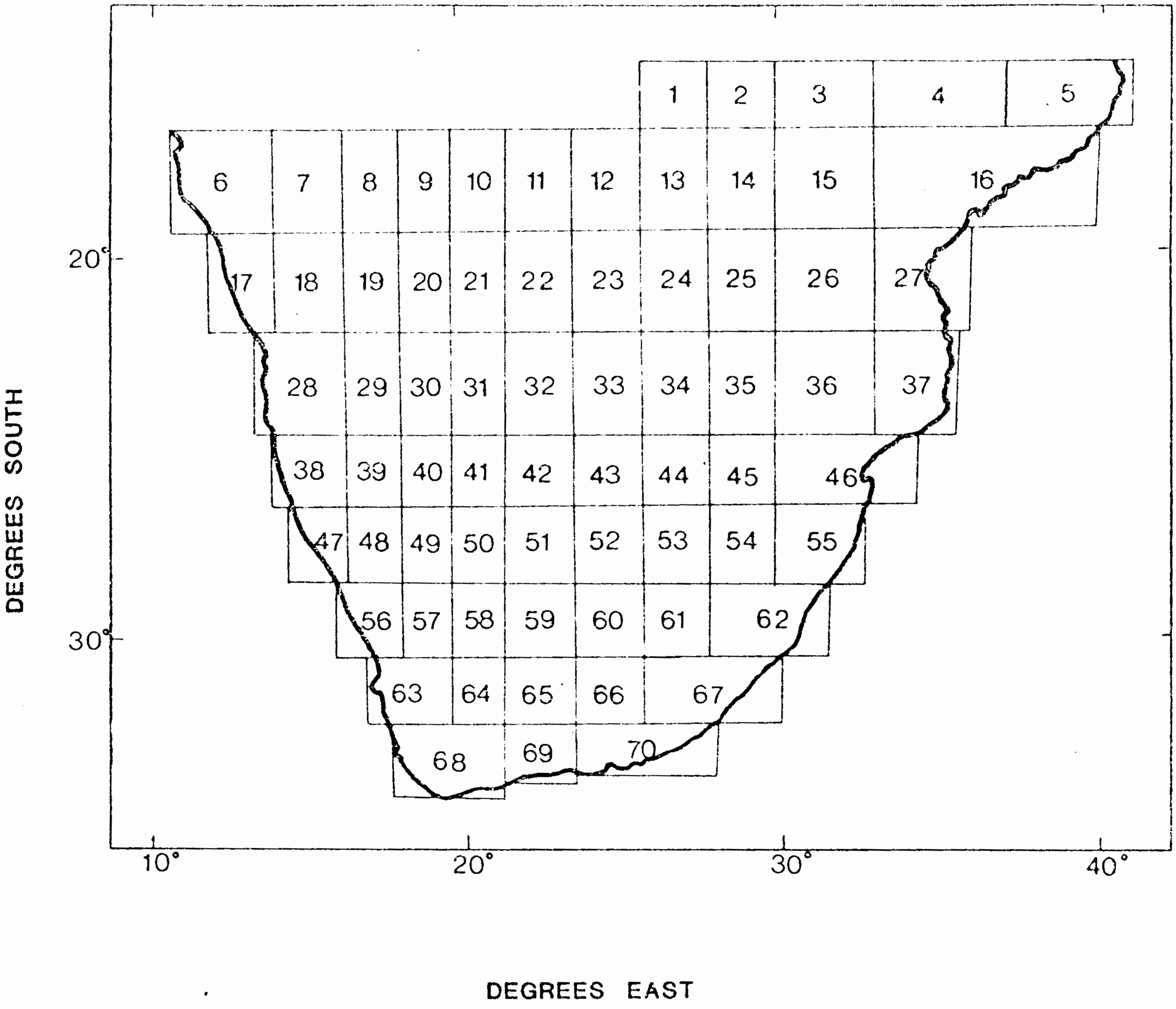
Animal-facilitated plant dispersal systems have until recently been thought to be relatively poorly developed in temperate areas (Snow 1971; Morton 1973; Howe & Estabrook 1977); a view largely based on temperate fruits being nutritionally less rewarding than tropical fruits (Snow 1971; White 1974). This view is, however, not supported by results obtained on frugivory in temperate Spain (Herrera 1981; Herrera & Jordano 1981).

In southern Africa considerable latitudinal variation in climate exists with the northern parts being tropical and southern parts temperate. Further, rainfall patterns assume a north-south alignment, dividing the subcontinent into relatively mesic eastern and xeric western sectors. In this study the geographical distributions of tree species possessing different fruit types and dispersal agents in relation to the three gradients (tropic-temperate, mesic-xeric and specialist-opportunist) are compared. The results derived from these distributional criteria are compared with predictions in the literature (Van der Pijl 1969a & b; Snow 1971; McKey 1975).

MATERIALS AND METHODS

Based on information extracted from distribution maps (Coates Palgrave 1977) and cluster analysis techniques described fully in Knight, Crowe & Siegfried (1982), a grid of 70 quadrats (Fig. 1) was used to analyse the spatial distribution of defined subsets of species of the total indigenous southern African angiosperm tree flora (1 340 species). The subsets are those species possessing drupe, berry, pod, capsule and nut fruit types, together with subsets of species dispersed by birds, mammals, and wind. The interpretations of the cluster analyses are standardized *a priori* at a 25% similarity level for direct comparison between the subsets. Proportional species richness (defined as the percentage of any specified subset of species in the total indigenous angiosperm tree flora) is represented as a two-dimensional contour surface (S.G.P. Diederiks 1979), and analysed for spatial dependence (or randomness) in preset directions through spatial autocorrelation (Cliff & Ord 1969, 1973; Ward 1978; Chessel 1981).

Fig. 1. The grid (70 quadrats) used in analysing the distribution of subsets of species bearing eight different fruit types of the total southern African indigenous tree flora.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DEGREES SOUTH
DEGREES EAST

RESULTS

Species with fleshy fruits

Species bearing drupes and berries clustered into eight regions (B, E, P, N, R, O, K, L) and seven regions (B, E, L, N, O, P, Q), respectively (Figs 2a, 2b, 3a and 3b). The smaller Western (O) and Eastern Bushveld (N) regions occupied by the berry-bearing subset of species are compensated by larger Karoo (E) and Afromontane (B) zones, respectively. A Kalahari (P) region is present in both subsets, although displaced more easterly in drupe-bearing species. In both of these subsets and in the "all fruit types" subsets (Figs 2c & 3c), fragmentation of similarity patterns occurs along the west coast which may reflect the relatively low number of species in this area. The Northern Namib (L) is combined with the Central South Namib (K) in berry-bearing species, whereas in drupe-bearing species the Namaqualand (Q) is combined with the Central South Namib (K). The combination of berry and drupe-bearing species appears to be most influential in determining the "all fruit types" pattern.

There is a tendency for drupe-bearing species to predominate in the western sectors of the subcontinent (Fig. 4a). Berry-bearing species attain maximum proportional species richness as two peaks in the eastern sectors of the subcontinent (Fig. 4b) within region B.

A normal distribution of proportional species richness for drupe and berry bearers among the quadrats can be assumed (Table 13). For drupe-bearing species, the greatest degree of spatial dependence exists in a N-S direction; NW-SE and NE-SW directions being non-dependent (Table 14). Spatial dependence exists for

Fig. 2. Dendrograms formed by the Bray-Curtis (1957) similarity coefficient and group average sorting (Field & McFarlane, 1968) of the subsets of species possessing different fruit types and dispersal techniques. The following dendrograms represent species bearing (a) drupes, (b) berries, (c) all fruit types, (d) pods, (e) capsules, (f) nuts, (g) wind-dispersed fruits, (h) bird-dispersed fruits and (i) mammal-dispersed fruits. The names of the regions identified at a 25% similarity are:- A = Bushveld, B = Afromontane, C = False Upper Karoo, D = West Coast Karoo, E = Arid Karoo, F = Eastern Botswana, G = South-west Cape, H = Eastern Kalahari, I = Western Kalahari, J = Bushveld- Karoo Transition, K = Southern Central Namib, L = Northern Namib, M = Subtropical coastal, N = Eastern Bushveld, O = Western Bushveld, P = Kalahari, Q = Namaqualand, R = Zambezian.

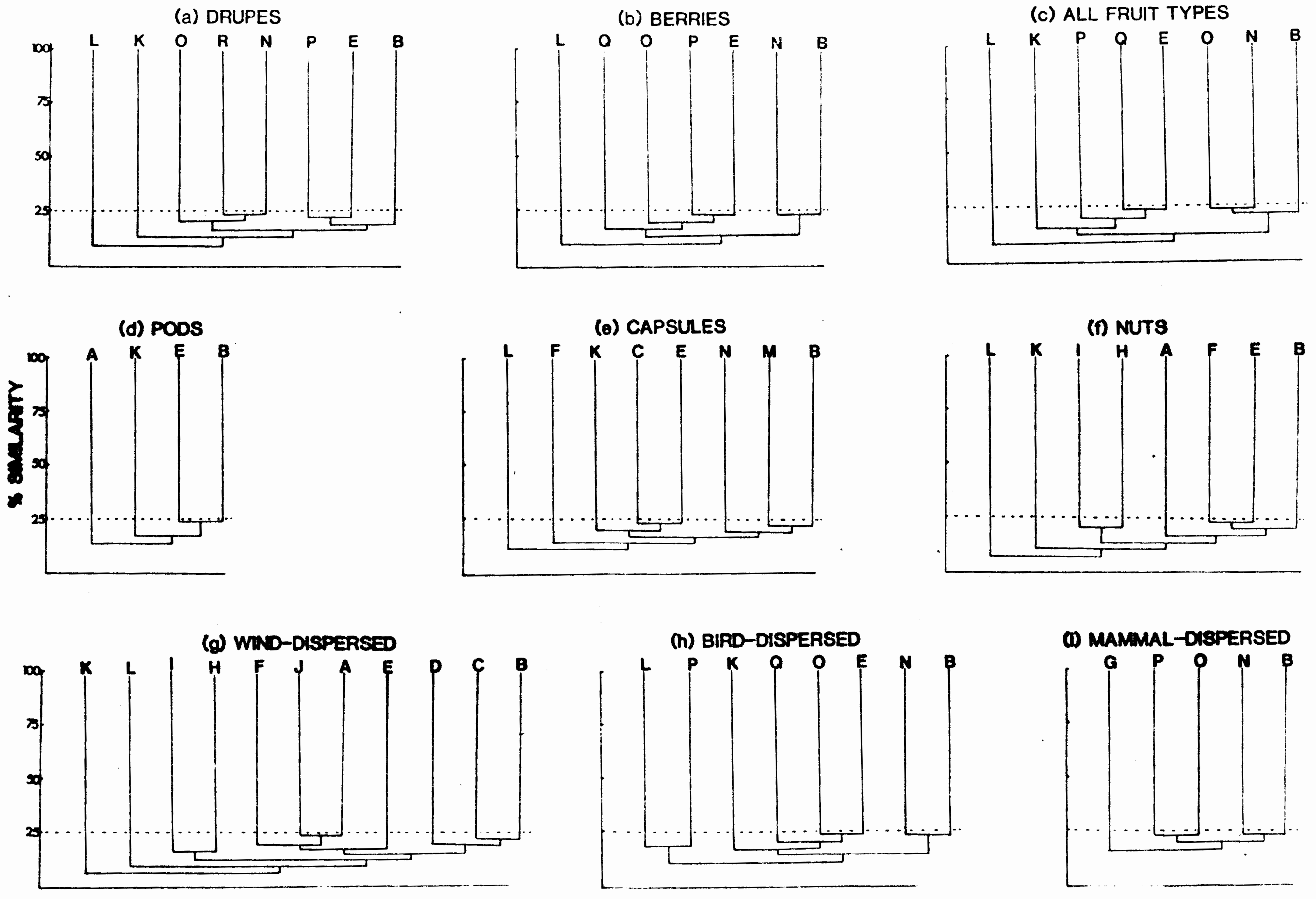
(a) DRUPES
L K O R N P E B
(b) BERRIES
L Q O P E N B
(c) ALL FRUIT TYPES
L K P Q E O N B
(d) PODS
A K E B
(e) CAPSULES
L F K C E N M B
(f) NUTS
L K I H A F E B
(g) WIND-DISPERSED
K L I H F J A E D C B
(h) BIRD-DISPERSED
L P K Q O E N B
(i) MAMMAL-DISPERSED
G P O N B
% SIMILARITY
100
75
50
25

Fig. 3. Cartographic representation of the dendrograms in Fig. 2. for subsets of species possessing different fruit types and dispersal techniques. The following maps represent species bearing (a) drupes, (b) berries, (c) all fruit types, (d) pods, (e) capsules, (f) nuts, (g) wind-dispersed fruits, (h) bird-dispersed fruits and (i) mammal-dispersed fruits. The names of the regions identified at a 25% similarity are:- A = Bushveld, B = Afromontane, C = False Upper Karoo, D = West Coast Karoo, E = Arid Karoo, F = Eastern Botswana, G = South West Cape, H = Eastern Kalahari, I = Western Kalahari, J = Bushveld- Karoo Transition, K = Southern Central Namib, L = Northern Namib, M = Subtropical coastal, N = Eastern Bushveld, O = Western Bushveld, P = Kalahari, Q = Namaqualand, R = Zambezian. The hatched areas indicate a lack of data.

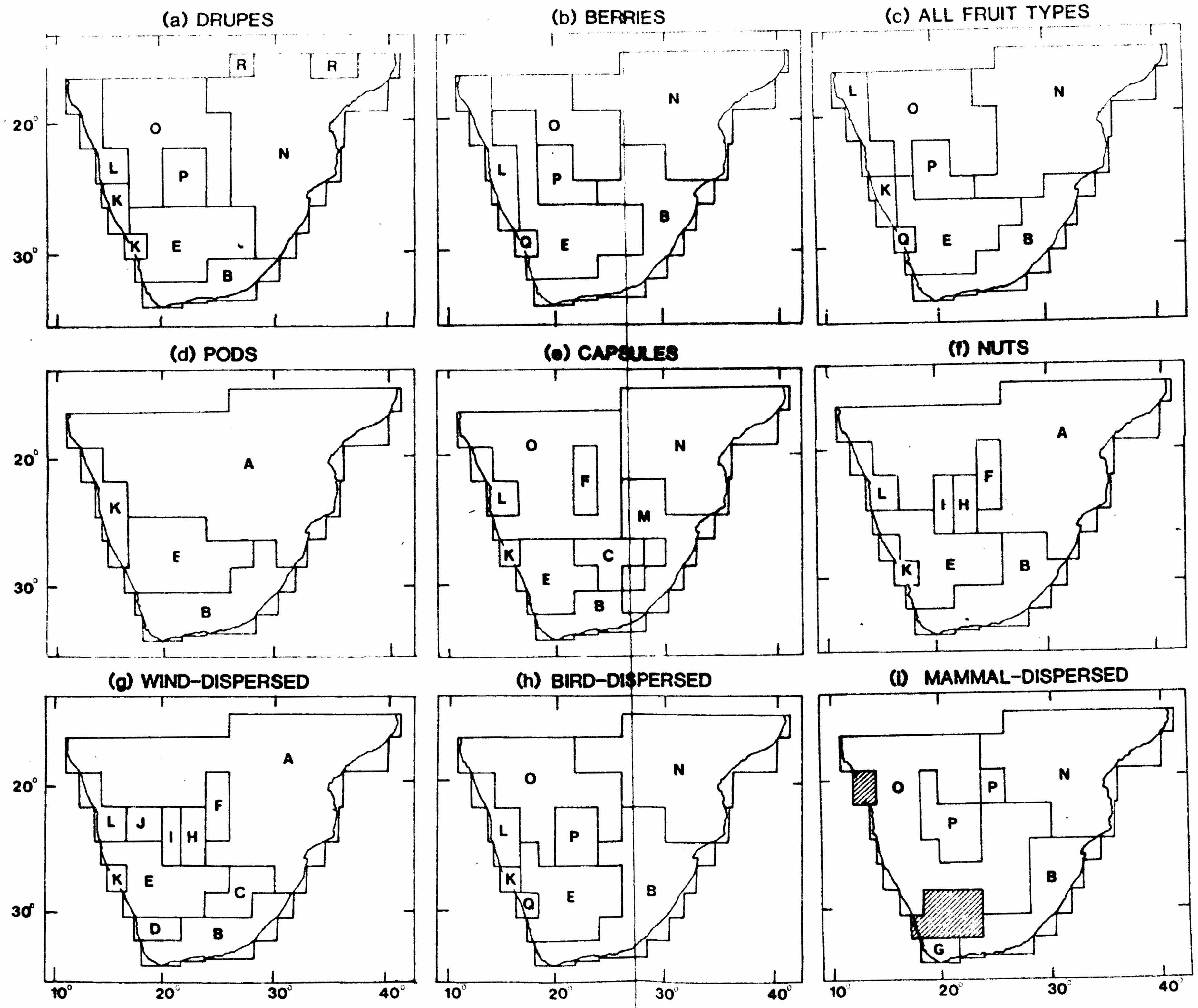
(a) DRUPES
(b) BERRIES
(c) ALL FRUIT TYPES
(d) PODS
(e) CAPSULES
(f) NUTS
(g) WIND-DISPERSED
(h) BIRD-DISPERSED
(i) MAMMAL-DISPERSED
20°
30°
10°
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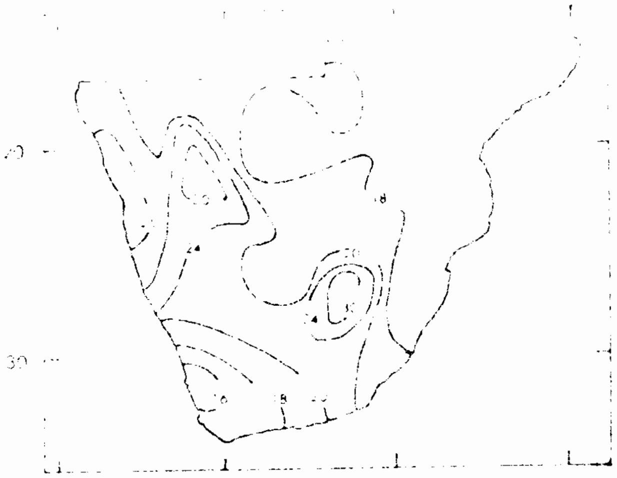
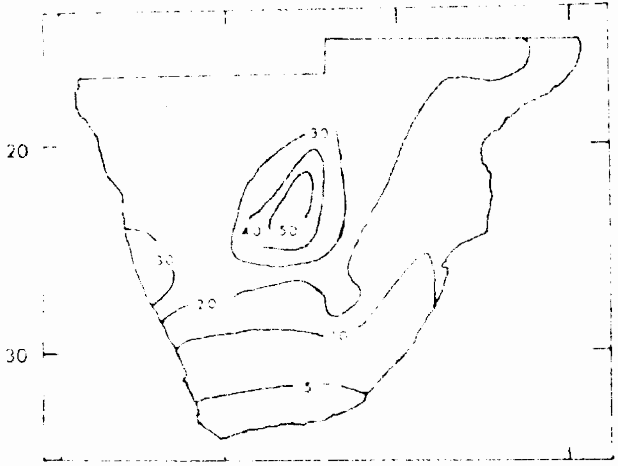
Fig. 4. Proportional species richness for each subsets of species possessing different fruit types and dispersal techniques. The following maps represent species bearing (a) drupes, (b) berries, (c) pods, (d) capsules, (e) nuts, (f) wind-dispersed fruits, (g) bird-dispersed fruits and (h) mammal-dispersed fruits. All numbers are percentages.

(a) DRUPES

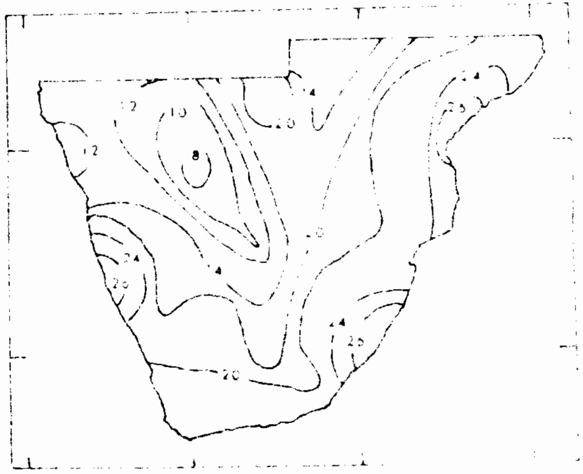


(b) BERRIES

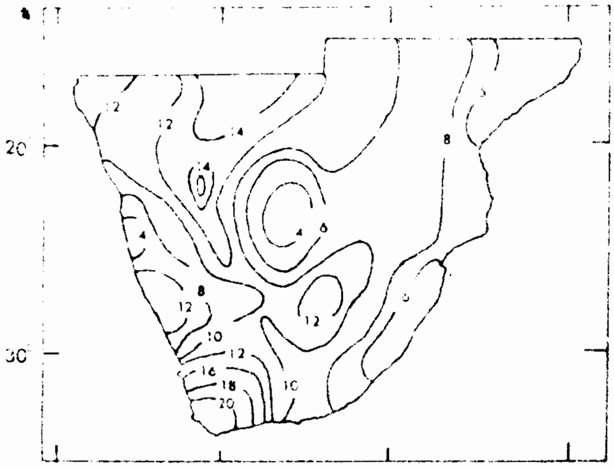
(c) PODS



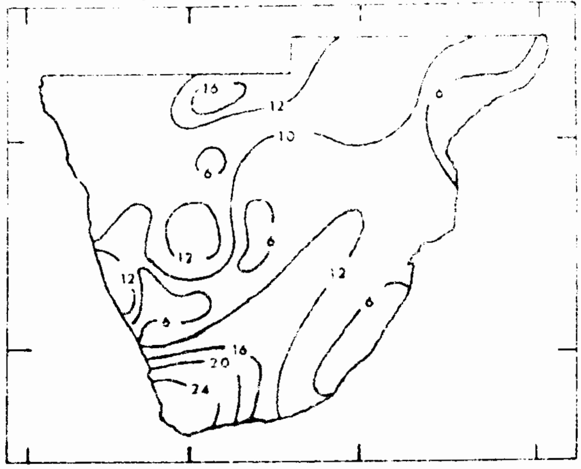
(d) CAPSULES



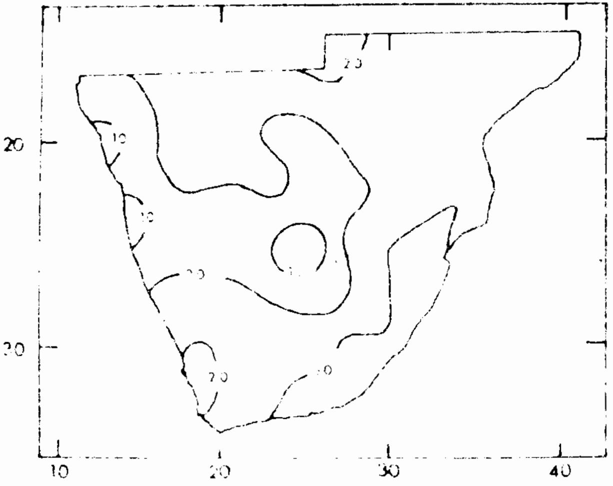
(e) NUTS



(f) WIND-DISPERSED



(g) BIRD-DISPERSED



(h) MAMMAL-DISPERSED

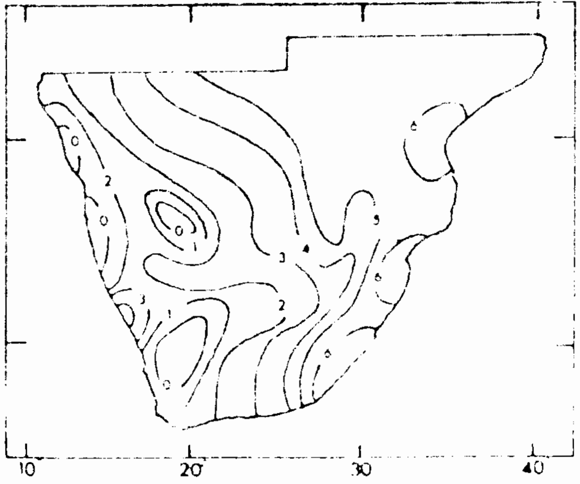


Table 13. Results of coefficient of kurtosis, to determine the degree of normality in the data on proportional species richness of the fruit types within the southern African tree flora

Species subset	Coefficient of Kurtosis
Berry	2,95
Drupe	2,95
Nut	4,60
Capsule	2,32
Pod	4,40
Wind-dispersed	5,80
Bird-dispersed	2,82
Mammal-dispersed	1,45

For a normal distribution the coefficient of Kurtosis is 3,00.

Table 14. Results of the spatial autocorrelation statistic (*r*) for proportional species richness of southern African tree species which posses drupe, berry, pod, capsule and nut fruits in four directions as well as overall

Direction	Statistic	Berry	Drupe	Nut	Capsule	Pod
N-S	*r*	0,63	0,49	0,29	0,58	0,75
	z	(4,98)	(3,90)	(2,40)	(4,62)	(5,99)
E-W	*r*	0,68	0,34	0,42	0,65	0,80
	z	(5,44)	(2,85)	(3,43)	(5,21)	(6,43)
NW-SE	*r*	0,46	0,24	0,23	0,48	0,52
	z	(3,53)	(1,91)	(1,86)	(3,65)	(4,02)
NE-SW	*r*	0,60	0,22	0,12	0,47	0,72
	z	(4,66)	(1,79)	(1,06)	(3,61)	(5,56)
ALL	*r*	0,60	0,33	0,27	0,55	0,70
	z	(9,74)	(5,48)	(4,60)	(8,95)	(11,42)

Critical values of absolute value (*z*) for significance levels are : *z* = 2,00 *P*= 0,05; *z* = 3,00 *P* = 0,01, berry-bearing species in all directions (Table 14), the E-W direction appearing to have the most regular, and the NW-SE direction the least regular pattern of change.

Species with dry fruits

Pod-bearing species clustered into four regions (A, B, E, K), whereas capsule and nut bearing species clustered into eight regions (B, C, E, F, K, L, M, N), (A, B, E, F, H, I, K, L) respectively (Figs 2d, 2e, 2f, 3d, 3e, 3f). Pod-bearing species have the simplest pattern (Figs 2d & 3d), with an expansive Bushveld region (A), and a single consolidated west coast region (L). The pattern for capsule-bearing species is more complicated (Figs 2e, 3e), with an extensive Eastern Bushveld (N), but no Kalahari region. The Afromontane that existed in species possessing fleshy fruits is split into Temperate Cape (B) and Subtropical Coastal (M) regions, and a False Upper Karoo region (C) also exists. A reduced Karoo (E) region results with the fragmentation of species similarity patterns in the eastern temperate parts of the subcontinent. Both North and South Central Namib regions (L, K) exist, the latter showing some affinities with the reduced Karoo (E) region. The Bushveld (A), Karoo (E) and Afromontane (B) regions are similar and common to the patterns of pod-bearing species, while the Namib regions (K, L) are similar to the pattern of capsule-bearing species. The nut-bearing species possess a Kalahari region, (Figs 2f & 3f), which unlike the fleshy fruits is divided into Eastern (H) and Western (I) sectors.

A pronounced peak in the proportional species richness of pod-bearing species occurs in the interior Kalahari depression (within region A), and a much smaller peak occurs along the western coast of S.W.A/Namibia (Fig. 4c). A pronounced N-S trend, with a depauperate southern part, is superimposed over this pattern. The pattern for capsule-bearing species is more complicated (Fig. 4d), with three peaks apparent (each 26%), two of which are located along the eastern coast (one each in regions M and N) and one along the central S.W.A/Namibia coast (between regions L and K). The lowest proportion of capsule-bearing species is found in the central Kalahari (within region O), almost exactly where the peak in pod-bearing species occurs. The proportional species richness of nut-bearing species (Fig. 4e) shows a pronounced concentration in the south-western corner (region B) of the subcontinent, and a smaller peak is found (within region A) near the northern S.W.A/Namibia-Botswana border.

All three dry fruit types were assumed to possess non-normal distributions (Table 13). Spatial dependence existed in all directions for both pod and capsule-bearing species. In the former, however, the degree of spatial dependence is considerably higher (Table 14), supporting the notion that pod-bearing species have a relatively simple and regular spatial distribution. The E-W direction is the most regular pattern for all of these fruit types, whereas the NW-SE and the NE-SW directions are the least regular patterns for species with pods and capsules, respectively. No spatial dependence exists in the NE-SW and NW-SE for the nut-bearing species.

Species with wind, avian and mammalian dispersal

Species which are dispersed either by wind, birds or mammals clustered into eleven (A, B, C, D, E, F, H, I, J, K, L), eight (B, E, K, L, N, O, P, Q) and five (B, G, N, O, P) regions, respectively (Figs 2g, 2h, 2i, 3g, 3h and 3i). The pattern of wind-dispersed species has features which correspond with that for species bearing nuts: a single Bushveld region; a Karoo region (except for presence of a West Coast Karoo); division of the Kalahari region into eastern and western sectors; and, separation of North and South Central Namib regions (L & K). The pattern for bird dispersed species is very similar to that for species bearing berries, with only the following differences: a Northern Namib region that does not extent so far south, but a separate Southern Central Namib exists; an Arid Karoo region that does not extend so far north; and, the Kalahari region has a more easterly displacement. The pattern for species dispersed by mammals is very different to the other patterns in that no Karoo areas are present and large Kalahari and small South-western Cape (G) regions exist.

The pattern for species bearing wind-dispersed fruits shows a very pronounced peak in the south-western corner (in region B) of the subcontinent (Fig. 4f), with a smaller peak in northern S.W.A/Namibia (within region A) and pronounced 'lows' along the east coast. The patterns for species bearing bird-dispersed fruits (Fig. 4g) have peaks along the south-eastern coast (almost exclusively in region B), whereas the western portions of the subcontinent are noticeably depauperate (region L). The proportional species richness for mammal-dispersed species (Fig 4h) shows a very similar pattern, although the eastern peaks are closer to the coast.

The NE-SW and NW-SE directions have no spatial dependence for species bearing wind-dispersed fruits (Table 15). The direction with the most regular pattern change for these species apears to

Table 15. Results of spatial autocorrelation for proportional species richness of species which possess fruits dispersed by wind, bird and mammal agents in four directions as well as overall

Direction	Statistic	Wind	Bird	Mammal
N-S	*r*	0,28	0,70	0,69
	z	(2,30)	(5,53)	(5,36)
E-W	*r*	0,41	0,66	0,66
	z	(3,44)	(5,31)	(5,36)
NW-SE	*r*	0,22	0,44	0,66
	z	(1,75)	(3,37)	(4,97)
NE-SW	*r*	0,13	0,69	0,49
	z	(1,01)	(5,30)	(3,79)
ALL	*r*	0,26	0,63	0,63
	z	(4,51)	(10,21)	(10,12)

Critical values of absolute value (*z*) for significance levels are : *z* = 2,00 *P*= 0,05; *z* = 3,00 *P* = 0,01, be E-W. For species bearing fruits dispersed by birds or mammals all directions are spatially dependent. However, the NW-SE and NE-SW directions have the least and the N-S directions the most regular patterns of change in both subsets of dispersers.

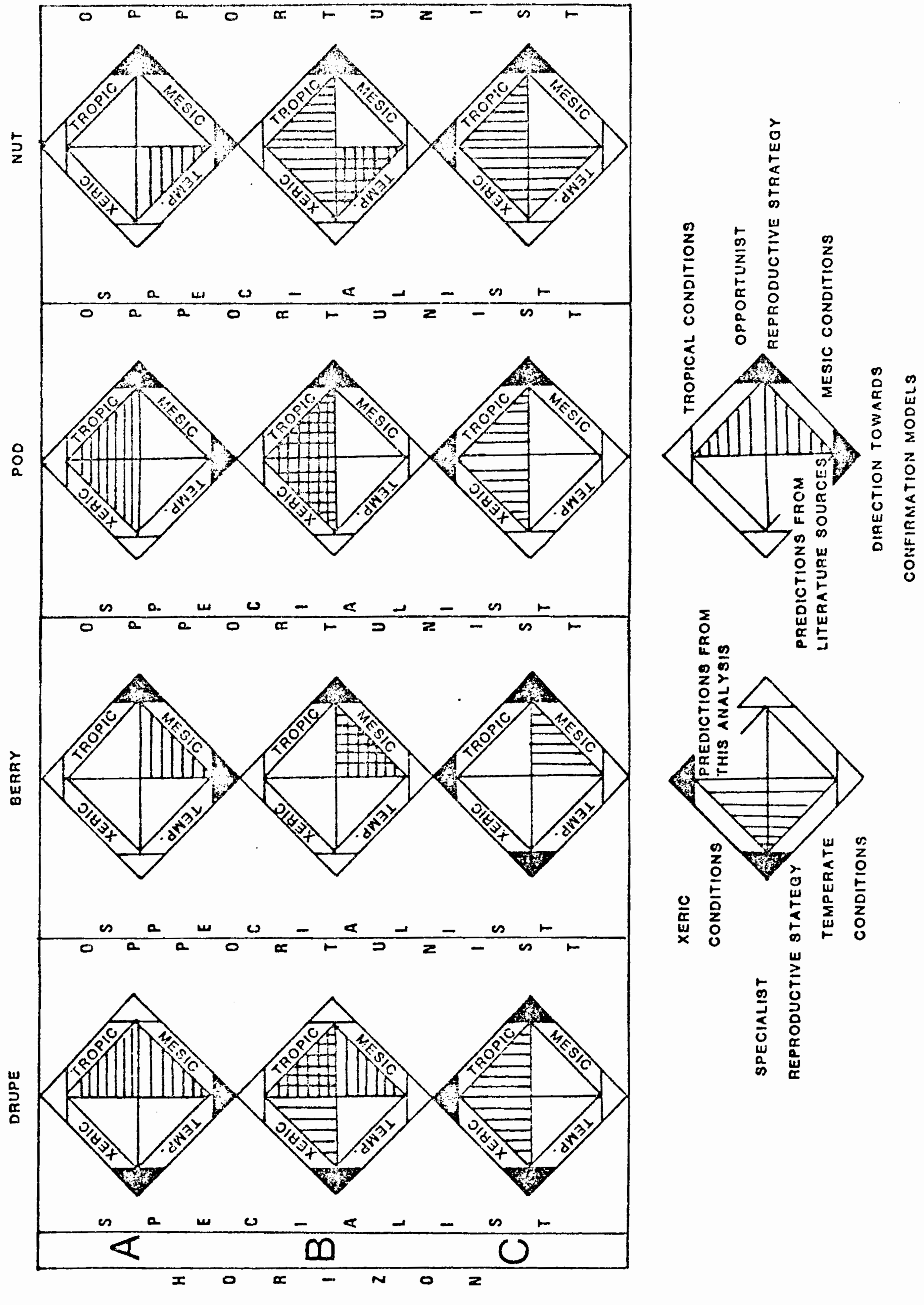
DISCUSSION

The combination of tropical-temperate (N-S) and mesic-xeric (E-W) gradients may be responsible for diagonal directions (NE-SW) having the least spatial dependence (Table 14 & 15) in most of the subsets of species. Further, most species similarity patterns possess regions which orientate latitudinally and longitudinally. The exception is provided by species bearing nuts and pods, the latter tending to align only in a latitudinal direction. It, therefore, is apparent that strategies for dispersal based on morphological attributes are not uniform over the subcontinent. Van der Pijl (1969a & b), however, hypothesized that less specialized strategies exist in less predictable environments. The inter-relationships between the two environmental gradients and a reproductive gradient for each fruit type are represented in Fig. 5. Horizon A represents the literature predictions, horizon C the results derived from distributional analyses, and horizon B the areas where the above two predictions conform.

Drupes

Fig. 5 indicates that species bearing drupes are likely to predominate in tropical mesic conditions (where seasonal fluctuations of precipitation and temperature are minimal), while the reproductive strategy will tend towards a specialist mode. The results indicate that these species predominate in the drier

Fig. 5. A schematic representation of the inter-relationships of the three gradients (tropic-temperate, mesic-xeric and opportunist-specialist) that may affect seed dispersal in four subsets of species (possessing drupe, berry, pod and nut fruits). Horizon A represents predictions derived from literature sources, horizon C predictions derived from the distributional analyses of southern African indigenous tree species, and horizon B areas where the two predictions conform.


DRUPE
BERRY
POD
NUT
A
B
C
HORIZON
SPECIALIST
OPPORTUNIST
TROPIC
MESIC
XERIC
TEMP.
XERIC CONDITIONS
SPECIALIST REPRODUCTIVE STATEGY
TEMPERATE CONDITIONS
PREDICTIONS FROM THIS ANALYSIS
PREDICTIONS FROM LITERATURE SOURCES
TROPICAL CONDITIONS
OPPORTUNIST REPRODUCTIVE STRATEGY
MESIC CONDITIONS
DIRECTION TOWARDS CONFIRMATION MODELS

areas, but confirm the tropical aspects of their distribution. For dispersal in xeric conditions a propensity for an opportunistic reproductive strategy is hypothesized (Van der Pijl 1969a) which conflicts with the predicted strategy for drupe-bearing species. This apparent conflict may be the result of a depauperacy of certain families (e.g. Lauraceae and Palmae) which possess drupaceous fruits (Snow 1981). It has been hypothesized that such elements existed in forests which occupied considerable areas of the subcontinent under the southward extension of the tropical rainfall system (Snow 1981). Intervening periods of colder conditions (glacial times) cut off the supply of moist tropical air, causing arid corridors to exist from S.W.A/Namibia to northern Tanzania (Van Zinderen Bakker 1969; Verdcourt 1969), and may have excluded these families which, incidentally, are still well represented in the Canary Islands and Madagascar. If one assumes that the species bearing drupes evolved before species bearing berries (the drupe morphology being more analogous to the carpel and arillate fruits of some primitive families) they would have had longer and more frequent exposures to the aridity of glacial times, and become better adapted to this regime. The large single stone, usually considered an adaptation for seedlings in tropical forests, may also represent a pre-adaptation for the prolonged seed dormancy that is usually required in arid areas. Although a depauperacy of drupe-bearing tree species occurs in the higher latitudes, many shrubs along the arid west coast (Strandveld) of southern Africa possess drupaceous fruits (pers. obs.). These fruits possess rather large and very hard seeds with pericarps of an extremely high water content, thus conflicting markedly with existing theories.

Berries

In Fig. 5 the theories derived from the literature indicate that species bearing berries should occur in both tropical and temperate mesic areas, while the reproductive strategy is likely to be opportunistic. The results derived from the analyses confirm the distributional aspects of these predictions. The intensity of peak frequency along the moist east coast regions, however, was not expected. There is a predominance of berry-producing species in most of the true forests of the subcontinent. Berry-producing species apparently are more numerous than drupe-producing species in the dune forests of Mtunzini (Frost 1980). A possible explanation may be linked to the seasonal nature of the humid forests which in the past may have had successive recolonizations after the disruptions of the glacial periods. The small seeds of berries may be advantageous during a recolonization phase, but are unlikely to have the potential dormancy that large seeds might possess. Although multiple seeds usually will be small in size, they can become quite large when a small number of seeds is accommodated within a large sized fruit, e.g. _Ekebergia capensis_. These fruits could almost be considered to be drupaceous and may reflect a specialist reproductive strategy. On the other hand, some species which may be structually drupaceous (but derived from a berry) may be accompanied by unnutritious pericarps, e.g. _Mimusops caffra_ and _Euclea natalensis_ (Frost, 1980). It is therefore felt that neither a specialist nor an opportunist strategy can be rigorously applied, and a two-way arrow (Fig. 5) was drawn for species which produce berries and drupes.

Pods

The likely tropical arid distribution of these species appears to be confirmed (Fig. 5). An anomalous feature, however, is the total lack of pods in the western low latitudes. A possible explanation could be the paucity of mammalian dispersers under extreme xeric conditions, or that these types of fruit evolved in the east and have subsequently progressed westwards. This process, together with a more mesic pleistocene Southern Namib (Tankard & Rogers, 1978), and hyper-arid corridors in the Kalahari may have allowed the pod-bearing species to have reached the west coast and have remained in this area along dry riverbeds where subterranean water is present. The Northern Namib may never have been mesic since the Oligocene (Van Zinderen Bakker, 1975), and consequenly has never been invaded by pod-bearing species. The Northern Namib is the most isolated region in terms of species composition and relatively few species occur in each of the genera (Knight et.al 1982; Robinson 1978); conditions that are considered indicative of antiquity but not of rapid speciation (Stebbins 1972). Under favourable conditions, however, dispersal of pod-bearing species by mammals can be rapid, as reflected by the spread of the alien pod-bearing Mesquite (Prosopis glandulosa) over the drier parts of the subcontinent (Harding 1978).

Nuts

The biotic dispersal of nut fruits has been considered to be an effective pioneering strategy in the temperate areas, although a large quantity of seeds may be required (Van der Pijl 1969a; Snow 1971). The present climate of southern Africa is probably too mild to promote the requirements necessary for this strategy; namely, widespread hibernation of mammals and the accumulation of nut caches. The seeds of fleshy fruits are, however, scatter horded by southern African squirrels, and this might be the prototype for modern nut caches in temperate areas. Most nut-bearing species in southern Africa are dispersed by wind. Usual modifications include a reduction in physical size, an increase in seed production and the development of 'wings' or 'tufts' (Snow 1971), and therefore an opportunistic dispersal in pioneer vegetation. Wind dispersal of propagules is unlikely in tropical forests, unless in top-storey species. These species are usually a large component in temperate forests. The most temperate parts of the subcontinent have a large component of nut-bearing species, thus confirming the literature predictions (Fig. 5). The pronounced nature of this peak may be due to the glacial periods when the Podocarpus forests were extensive and climate became sufficiently severe to evolve or support widespread nut caching. Milder climates may have been the stimulant for the widespread evolution of wind-dispersal. There is a smaller peak of nut-bearing species in the tropical but arid S.W.A/Namibia, apparently a contribution from the genus Combretum. Dry winged-fruits may be pre-adapted to arid conditions, since there is no relianace placed on a population of biotic dispersal agents, and seeds may have a good dormancy potential.

Capsules

Species bearing capsules seem to have the most diversified techniques for dispersal, and include tufted, winged, and very small seeds for wind dispersal. Some capsules contain sticky seeds, seeds surrounded by edible pulp, and arillate seeds which are all likely to be dispersed by birds, and the large indehiscent capsules may be dispersed by larger mammals. The confused spatial patterns that result from the analysis of this group of species may be a reflection of such diversified morphological forms.

Species dispersed by known agents

The evolution of plant-animal dispersal relationships is believed to be the result of reciprocal exploitation by the two parties. The system being subjected to opposing selective pressures leads to continuous feedback and compromise situations (Snow 1971). The results of tropical-based research (Howe & Estabrook 1977) indicate that this compromise falls between two extremes when the agents involved are birds: a high quality, nutritious, expensive fruit to "pay" for the services of a reliable disperser ("specialist"), as opposed to the inexpensive fruit which rewards the unreliable dispersers ("opportunist"). The expensive fruit is considered to be accompanied by a large seed (viz "drupaceous") which acts as ballast and facilitates rapid evacuation once the fleshy pericarp has been digested in the bird's gut (McKey 1975). The specialist rich fruit-based systems are considered to be particularly common in the tropics, as opposed to temperate habitats where environmental limitations may be responsible for the evolution of "unspecialized" poor-fruit based plant-bird systems (Snow 1971; Morton 1973; Howe & Estabrook 1977).

Thus, the results of the analysis could be expected to predict bird-dispersed fruits to correspond with the drupe fruit species patterns in the tropics and the berry-bearing species in the temperate areas. It was found, however, that the bird-dispersed fruits showed high conformity with the pattern for berry-bearing species irrespective of latitude. The concept of large single seed and small multi-seededness being related to the nutritional value of the pericarp is also questioned. It is possible that while drupe-bearing species evolved to occupy more xeric areas, the berry-bearing species evolved in the tropical and subtropical forests and assumed the properties of drupes and their dispersal syndrome. Africa is, however, considered to possess few avian specialist frugivores (Snow 1981), a condition that may have resulted from the aridity experienced during glacial periods.

The spatial patterns of mammal dispersed fruits indicate a great depauperacy of species in the higher latitudes and in the extreme arid areas, and may be a reflection of the lack of fruit-bats and frugivorous squirrels in these areas (Van der Pijl 1969a & b). Dispersal of fruit in southern Africa by browsing ungulates may have been reduced during the severest glacial periods when grassland probably replaced forest and bushveld. The intake of seeds contained within dry pods (<u>Acacia</u> spp.) may produce faster germination and reduce invertebrate seed predation (Lamprey, Halevy & Makachas 1974; Van der Pijl 1969a & b) and may represent mutual benefits to both parties. Most mammal-dispersed species, however, occurred in the forests along the east coast of the continent and are typically berry fruits with hard pericarps and seeds. The latter is probably a defence against the greater mastication of food by mammals. The specificity of relationships that exist between mammals and the dispersal of fruit has not been investigated as closely as for birds, and comparable coevolution theories have not been proposed, although the dispersal by the Aardvark may offer predictable and suitable germination sites for the seeds of some plants (Meeuse 1958).

CONCLUSION

(1) The predictions that drupe-bearing species will be most numerous under tropical mesic conditions is not supported by their biogeography in southern Africa, although a tropical distribution is confirmed. (2) The berry-bearing species were found to occupy mesic conditions irrespective of latitudinal influences and thus confirm the predictions. (3) The prediction that pod-bearing species will have tropical and xeric distribution is confirmed, although an anomalous paucity of species occurs in the low latitude western areas. (4) The nut-bearing species although predicted to dominate in temperate areas also occur under tropical xeric conditions, where an anemochorous dispersal method may be prefered if biotic agents are scarce. (5) Bird and mammal dispersed fruits showed little similarity with regard to each others biogeography. Those species dispersed by birds, however, showed a pronounced similarity to the biogeography of the berry-bearing species, while the biogeography of mammal dispersed fruits appears to be independent of fruit morphology.

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PART 3

QUANTIFIED HYPOTHESES FOR DESCRIBING RELATIONSHIPS BETWEEN FRUIT MORPHOLOGY IN SOUTHERN AFRICAN TREES AND ENVIRONMENTAL ELEMENTS

ABSTRACT

Hypotheses are advanced to relate fruit derivation, fruit size and fruit colour of southern African tree species to ten environmental variables. Stepwise multiple linear regression, canonical correlation and multidimensional contingency tables were applied to integrate these parameters. Berry, drupe and pod bearing species appear to be environmentally dependent, while fruit size and fruit colour although independent of each other are related to fruit type and the environmental variables.

INTRODUCTION

The dispersal of propagules of angiosperm plants may be reflected by a number of different fruit morphologies. Five categories of fruit morphology (drupe, berry, pod, capsule and nut) have been analysed in spatial terms for the southern African tree flora (see part 2), but each of these fruit morphologies may also be reflected in terms of environmental parameters. Quantified plant/environment relationships are usually defined by multiple linear regression analyses (Marrs & Bannister 1979). In this paper the use of canonical correlation (CCA), with its advantage of analysing all dependent (vegetation) and independent environmental variables [E] simultaneously, is evaluated as an alternative to linear regressions. Other morphological features such as fruit size [S] and colour [C] may also influence the dispersal properties of plants (See part 1). The possible environmental hypotheses defining the relationships between these properties are investigated with the aid of multidimensional contingency table models (MDC).

Data preparation

A grid of 70 quadrats (Fig. 1) was used to transform the distribution of each species in the southern African tree flora, extracted from Coates Palgrave (1977) into a numerical form (Knight et al. 1982). Further information on fruit type (drupe, berry, pod, nut & capsule), size (length in mm) and colour (white, red, orange, yellow, green, brown and black/blue/purple) was obtained from Palmer & Pitman (1972 & 1973), Palmer (1977) and van Wyk (1972 1974). The proportional species richness of each fruit type (defined as the percentage of fruit-bearing species in the total indigenous tree flora) was related to ten measures of the environment: mean annual solar radiation (XSR), mean annual temperature (XT), mean annual temperature range (XTR), January maximum temperature (JAMA), July minimum temperature (JUMI), mean annual rainfall (XRF), mean annual rainfall range (RRF), altitude range (RA), water surplus (WP) and actual evaporation (AE) for each of the 70 quadrats (Talbot & Talbot, 1960; Jackson, 1961; Thornthwaite, 1962; Clark, 1967; Schulze & McGee, 1978).

Statistical methods

The data were examined by means of canonical correlation analysis (Anderson 1958; Cooley & Lohnes 1971), using a BMDP P6M program. CCA performs an analysis between two suites of variables (dependent and independent) measured for each of the 70 quadrats. The dependent variables (fruit types) were transformed to a squared arcsine function (Fisher & Yates 1963). The CCA will give the maximum correlation that can exist between the sets of variables. A Bartlett's test defined the number of canonical variables necessary to explain the data, and is equal to the number of eigenvalues, such that the remaining eigenvalues are non significant. Confirmation tests using multiple linear regression analyses were also undertaken. To assess climatic influences on fruit type, colour, and size interactions multidimensional contingency tables (MCD) were derived. Each of the 10 environmental variables was categorized, by ranking the quadrats with respect to the value of the variable, and then dividing the 70 quadrats into five percentile groups of 14 quadrats each. The fruit size was categorized as < 15mm, 15-30mm and > 30mm. Two three-dimensional contingency tables for each environmental variable were defined: environment/colour/fruit type (the [ECF] table) and environment/size/fruit type (the [ESF] table). A single four-dimensional contingency table had too few expected frequencies in the fitted models; more than 20% of the cells had expected frequencies of less than 5. Each of these multidimensional contingency tables are an alternative to calculating each marginal total and its chi-square statistic. This technique involves the fitting of a hierarchical log-linear model of relationships and, thus, for the [ECF] table the full order of interactions between environment [E], fruit colour [C] and fruit type [F] in a three-dimensional contingency table may be defined as

$$\begin{aligned} \mathrm{Log}_e\, F_{ijk} &= \theta + \lambda_i^E + \lambda_j^C + \lambda_k^F \\ &\quad + \lambda_{ij}^{EC} + \lambda_{ik}^{EF} + \lambda_{jk}^{CF} \\ &\quad + \lambda_{ijk}^{ECF} \end{aligned} \tag{1,1}$$

The suffix j refers to the C (COLOUR) classification, and the term 'λ_j^C' will represent the contribution of C to the j th row of the table. For these models a $\underline{G}^2$ statistic is used as a measure for the goodness of fit (Brown 1977; Williams 1976). The smaller the $\underline{G}^2$ the better the fit of the model. The model which possesses the fewest 'λ' but fits the data so that the remainder not included in the model is non-significant, is used as a test against which other models are evaluated. For this analysis the BMDP P3F computer program was applied (Brown 1977).

RESULTS

The correlation coefficients among the dependent (5 fruit types) and independent variables (10 environmental measures) are represented as a correlation matrix (Table 16). Canonical correlation analysis (CCA) applied to the matrix reduced the situation until it could be explained by two canonical correlations. The larger of these correlations yielded a value of 0,7750 with $\chi^2 = 70{,}09$ (36 d.f.; $\underline{P} < 0{,}001$). The second resulted in a value of 0,7340 with $\chi^2 = 23{,}69$ (24 d.f.; $\underline{P} < 0{,}5$). For the first canonical correlation the corresponding coefficients applied to the set of independent variables leads to the definition of a linear function, say X where

$$X = -{,}153x_1 - {,}065x_2 + {,}918x_3 - {,}403x_4 + {,}479x_5 + {,}123x_6 - {,}115x_7 - {,}372x_8 \quad (2{,}1)$$
$$- {,}206x_9 - {,}425x_{10}$$

$x_1 - x_{10}$ are mean solar radiation, mean temperature range, mean temperature, January maximum temperature, July minimum temperature, mean annual rainfall, range in rainfall, range in altitude, water surplus and actual evaporation, standardized by measuring them about their respective means and divided by the respective standard deviations. The corresponding linear function for the dependent variables was found to be

Table 16 Correlation coefficient matrix of proportional species richness of tree species with five fruit types and 10 measures of the environment.

	Dependent Variables					Independent Variables									
	Berry	Drupe	Pod	Nut	Capsule	Mean solar rad.	Mean temp. range	Mean temp.	Jan. max. temp.	July min. temp.	Mean rain fall	Rain-fall range	Alt. range	Water surplus	Actual evap.
	BA	DA	PA	NA	CA	XSR	XTR	XT	JAMA	JUMI	XRF	RRF	AR	WP	AE
BA															
DA	-,389														
PA	-,730	-,041													
NA	-,049	,024	-,069												
CA	,692	-,205	-,750	-,200											
XSR	-,462	,532	,099	,080	-,178										
XTR	-,417	,445	,275	,147	-,435	,496									
XT	-,102	-,494	,514	-,101	-,288	-,463	-,062								
JAMA	-,159	,006	,295	,086	-,265	,098	,612	,455							
JUMI	,225	-,493	,008	-,168	,262	-,347	-,752	,421	-,269						
XRF	,578	-,438	-,341	-,134	,303	-,792	-,378	,181	-,126	,138					
RRF	,475	-,319	-,426	-,180	,410	-,394	-,446	,029	-,102	,288	,627				
AR	,440	-,046	-,577	-,139	,547	-,165	-,486	-,441	-,550	,089	,336	,415			
WP	,400	-,362	-,294	-,140	,362	-,470	-,454	,157	-,013	,275	,542	,481	,345		
AE	,521	-,379	-,292	-,105	,218	-,745	-,299	,163	-,155	,086	,949	,550	,263	,286	

Critical value of r for significance levels are: r = ,237, p = ,05; r = ,309, p = ,01; r = ,388, p = ,001.

$$Y = -,118y_1+,038y_2+,776y_3+,125y_4-,157y_5 \qquad (2,2)$$

where $y_1 - y_5$ are the proportional species richness of berry, drupe, pod, nut and capsule bearing fruits respectively.

These equations constitute the greatest correlation that can exist between any linear combination of the x's and any linear combination of the y's. From inspection of the linear combination of the x's (equation 2,1) it may be noted that x_3, x_4, x_5, x_8 and x_{10} are probably the most important coefficients representing the mean temperature, January maximum temperature, July minimum temperature, range in altitude and actual evaporation. For the linear combination of Y's the coefficients y_1, y_2, y_4 and y_5 are very small and may be approximated by zero, leaving only y_3, the pod bearing species. This would therefore seem to indicate that for the first correlation, pod-bearing species are positively related to mean temperature conditions but negatively related to seasonal extremes of temperature, actual evaporation and altitude range. From a multiple linear regression analysis (Allen 1973: STATJOB STEPREG1) used on these variables $\underline{Z}$ may be defined :

$$\underline{Z} = ,4517 + ,0438x_3 -,0190x_4 -,0153x_5 -,0001x_8 -,0002x_{10} \qquad (3,1)$$

This therefore explains 56% of the data. Inspection of the canonical loadings (correlations of the canonical variable with the original variable) for the pod-bearing species yielded a result of 0,970.

The second canonical variable can define a linear function for the independent variables such that

$$X = -,026x_1+.394x_2-,564x_3-,146x_4-,165x_5-1,037x_6+,119x_7-,001x_8 +,218x_9+ 0,473x_{10} \qquad (4,1)$$

where $x_1 - x_{10}$ are the same as for equation 2,1. The corresponding linear function for the dependent variables was found to be

$$Y = -,560y_1 +,697y_2 -,494y_3 +,159y_4 +,065y_5 \tag{4,2}$$

where $y_1 - y_5$ are the same as for equation 2,2. From the linear combinations of X's (3,1) it may be noted that x_6, x_3, x_{10} and x_2 are probably the most important coefficient representing mean annual rainfall, mean annual temperature, actual evaporation and mean temperature range. For the linear combination of Y's, y_2 and y_1 representing drupe and berry-bearing species, appear the most important coefficients. This would seem to indicate that in the second canonical correlation drupe and berry-bearing species are positively related to actual evaporation and negatively related to mean rainfall and temperature measures. However, the correlation matrix (Table 16) indicates the berry-bearing species to be positively correlated to mean annual rainfall, and actual evaporation, and therefore the high rainfall coefficient in 4,1 is probably explained by the drupe-bearing species, whereas the high actual evaporation coefficient is explained by berry-bearing species. Stepwise multiple linear regression analyses for drupe (5,1) and berry species (5,2) using these environmental variables yielded the following results.

$$\underline{Z} = ,5405 -,0001x_6 -,0148x_3 +,0001x_{10} -,0157x_2 \tag{5,1}$$

$$\underline{Z} = ,5884 -,0001x_6 +,0089x_3 -,0001x_{10} -,0057x_2 \tag{5,2}$$

with each equation explaining 47% and 43% of the data, respectively. The second canonical variable loadings yielded ,925 for drupe-bearing species and -,435 for berry bearing species.

From the results of the MDC analyses (Table 17) only six models for each environmental variable could be fitted and are represented in equations 6,1 to 6,6.

$$\mathrm{Log}_e\ F_{ijk} = \theta + \lambda_i^E + \lambda_j^S + \lambda_k^F + \lambda_{jk}^{SF} \qquad (SF,E)\ (6,1)$$

$$\mathrm{Log}_e\ F_{ijk} = \theta + \lambda_i^E + \lambda_j^S + \lambda_k^F + \lambda_{ji}^{SE} + \lambda_{jk}^{SF} \qquad (SE,SF)\ (6,2)$$

$$\mathrm{Log}_e\ F_{ijk} = \theta + \lambda_i^E + \lambda_j^S + \lambda_k^F + \lambda_{ki}^{FE} + \lambda_{kj}^{FS} \qquad (FE,FS)\ (6,3)$$

$$\mathrm{Log}_e\ F_{ijk} = \theta + \lambda_i^E + \lambda_j^C + \lambda_k^F + \lambda_{jk}^{CF} \qquad (CF,E)\ (6,4)$$

$$\mathrm{Log}_e\ F_{ijk} = \theta + \lambda_i^E + \lambda_j^C + \lambda_k^F + \lambda_{ji}^{CE} + \lambda_{jk}^{CF} \qquad (CE,CF)\ (6,5)$$

$$\mathrm{Log}_e\ F_{ijk} = \theta + \lambda_i^E + \lambda_j^C + \lambda_k^F + \lambda_{ki}^{FE} + \lambda_{kj}^{FC} \qquad (FE,FC)\ (6,6)$$

Where [SF, E] represents interaction of fruit type [F] and fruit size [S] and are each independent of the environment [E]. Similarly [SE, SF] represent a model that incorporates the interaction of fruit size with environment and the interaction of fruit type with fruit size. The model [FE, FS] represents fruit type-environment and fruit type-fruit size interactions, while [CF, E] represents colour [C]-fruit type interaction that are independent of the environment. The [CE, CF] model represents fruit colour-environment and colour-fruit type interactions, while the final colour-environment and colour-fruit type interactions, are represented by [FE, FC] model. The [FE, FC] and [FE, FS]

Table 17 Summary of six multidimensional contingency table models for each of 10 environmental variables (see Table 1). The values are a maximum likelihood statistic ($\underline{G}^2$) while the values in parentheses are the percentage of data explained by the model. An asterisk indicates the best fitting models in terms of maximum likelihood statistic and degrees of freedom (d.f.). N.M.F. indicates that no suitable model could be fitted to the data.

Table	FRUIT SIZE/FRUIT TYPE/ENVIRONMENT			FRUIT COLOUR/FRUIT TYPE/ENVIRONMENT		
Model	SF, E	SE, SF	FE, FS	CF, E	CE, CF	FE, FC
d.f.	56	48	40	136	112	120
XSR	N.M.F.	69,74 (95,36%)	45,39 (96,98%)*	135,28 (85,02%)	112,98 (87,49%)	79,62 (91,19%)*
XT	N.M.F.	46,68 (97,56%)	48,99 (97,44%)*	118,08 (89,57%)	93,02 (91,78%)	83,91 (92,59%)*
XTR	55,63 (96,60%)	36,44 (97,77%)	26,46 (98,38%)*	91,96 (90,86%)	77,20 (92,32%)	61,76 (93,86%)*
JAMA	33,91 (98,22%)	25,88 (98,65%)	13,66 (99,28%)*	52,31 (95,27%)	44,96 (95,94%)	34,00 (96,93%)*
JUMI	30,42 (98,32%)	18,69 (98,97%)	22,14 (98,78%)*	67,65 (94,03%)*	52,41 (95,38%)	57,96 (94,89%)
AE	46,70 (97,43%)	36,97 (97,96%)	15,27 (98,11%)*	76,42 (92,56%)	67,22 (93,45%)	43,76 (95,74%)*
RRF	68,47 (96,20%)	28,08 (98,44%)	34,36 (98,04%)*	95,76 (91,31%)	83,80 (92,40%)	64,47 (94,15%)*
AR	57,19 (96,96%)	29,46 (98,44%)*	38,18 (97,97%)	62,86 (94,42%)	50,55 (95,51%)	48,29 (95,71%)*
WP	64,85 (96,20%)	46,40 (97,28%)	27,89 (98,36%)*	90,88 (91,12%)	70,43 (93,11%)	57,90 (94,34%)*
XRF	42,90 (97,47%)	36,64 (97,83%)	19,03 (98,87%)*	82,93 (91,50%)	71,73 (92,65%)	58,83 (93,97%)*

models usually yielded the best results, although [CF, E] and [SF, E] are the most parsimonious fits (Table 17). This indicates that fruit type to environment, fruit type to colour and fruit type to fruit size are related. Further, those models that possess environmental independence ([CF, E] and [SF, E]) are only occasionally the best fitting models. This confirms the CCA where the environmental and the vegetative matrices are dependent on each other. The environmental models that explain most of the data, are January maximum and July minimum temperatures, mean annual rainfall and actual evaporation.

DISCUSSION

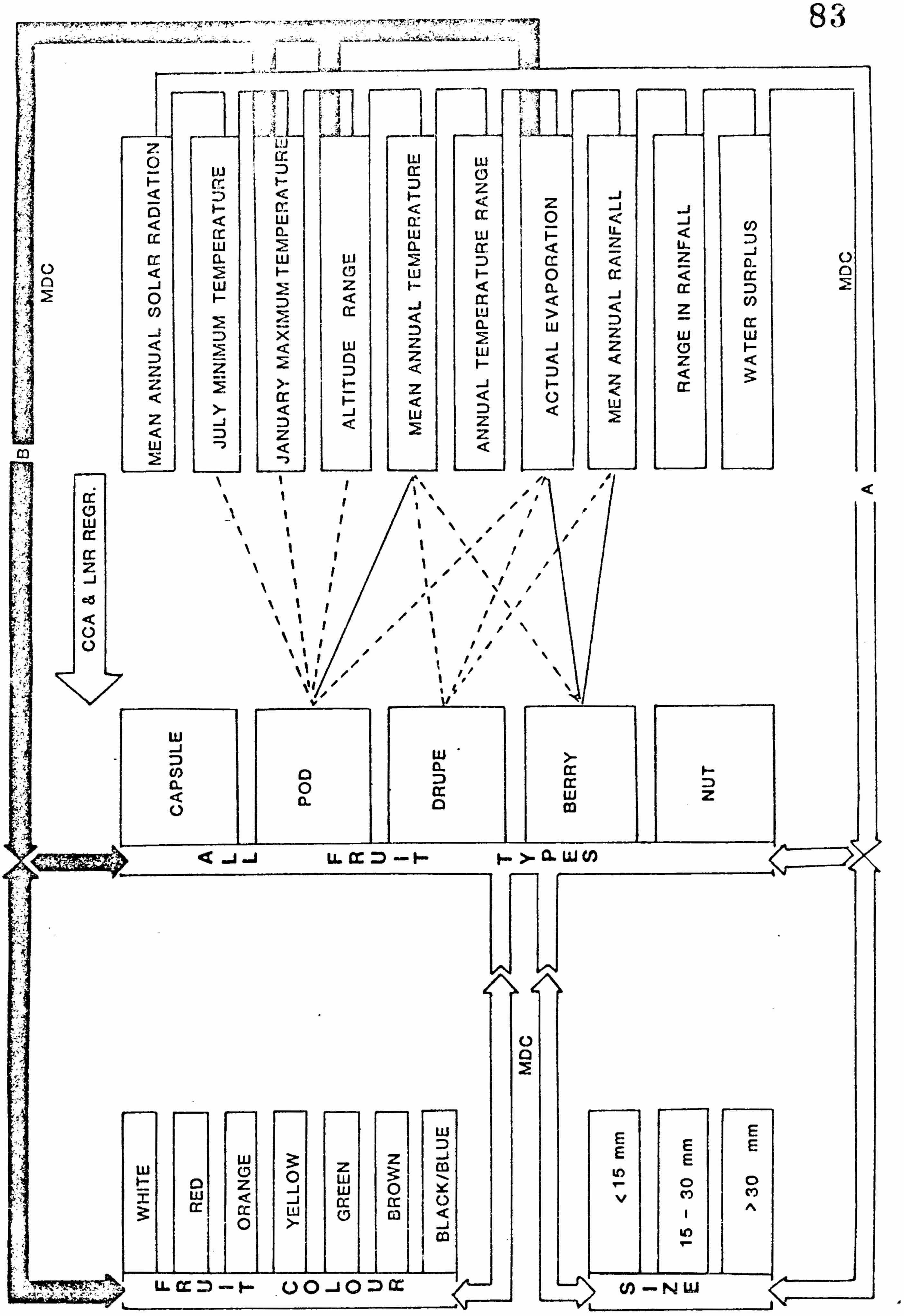
The ability to analyse vegetative and environmental data simultaneously has led to many applications of CCA (Gauch & Wentworth 1976). Promising results are, however, the exception while unsuccesful results are attributed to matrix singularity (Barkham & Noris 1970), a condition arising from variables not being independent of each other, and compounded by an increasing number of variables.

CCA and multiple linear regression analyses closely approximate one another with regard to identifying the fruit types that are environmentally determined, together with the variables that would influence these relationships. The multiple correlation coefficient for the linear regression on pod-bearing species of 0,7489 is not much less than the optimal correlation of 0,7750 derived from CCA, and may be indicative of minimal matrix singularity. Although the CCA identified both the drupe and berry-bearing species to be environmentally determined on a subset of independent variables (environment), the drupe-bearing species were far more closely correlated with the second canonical variable (berry: r = ,925 and drupe: r = -,435). From the linear regression it would seem that these two subsets of species are nearly equally determined on the subset of environmental variables. Herein lies a problem with the CCA; although both the drupe and berry-bearing species appear important in the second canonical correlation their relationship to some variables e.g. mean annual rainfall are diametrically opposed (drupes, r = -,438; berries, r = +,578). The simultaneous approach of CCA can conceal subtle but important relationships, and therefore this type of analysis should always be interpreted in conjunction with simple correlations (Barkham & Noris 1970).

In these MCD analyses, the relationship of fruit type to size were confirmed but fruit type to colour opposed a holistic model based on berry and drupe-bearing species presented in part 1. This ambiguity may be attributed to inclusion of five fruit types in this analysis. A re-analysed MDC including only drupe and berry-bearing species indicated much poorer fits (63 - 85%) for models including fruit type/colour relationships.

From a combination of these analyses a diagram of hypothetical relationships has been constructed (Fig. 6). On the left hand side of this figure are the relationships between all categories of fruit size, colour and fruit type derived from the MDC analyses. Fruit size and fruit colour are related to fruit type by bi-directional arrows, but fruit size and colour are unrelated. On the right hand side fruit type-environment relationship defined by CCA (where fruit types were tested against a suite of environmental variables) and MDC analyses (where a single environmental variable is tested with all five fruit types) are

Fig. 6. A hypothesized holistic model for relationships between fruit morphology (left) of southern African tree species and 10 environmental variables (right). Canonical correlation (CCA), linear regression (LNR REGR.) and multidimensional contingency tables (MDC) were used to define relationships. Under the CCA and LNR REGR. arrow the broken and solid lines indicate negative and positive environmental relationships respectively. In MCD analysis arrow (A) represents each enviromental element's relationship with fruit size and type, while the shaded arrow (B) indicates relationship with fruit colour and type defined at a 95% goodness of fit.


MEAN ANNUAL SOLAR RADIATION
JULY MINIMUM TEMPERATURE
JANUARY MAXIMUM TEMPERATURE
ALTITUDE RANGE
MEAN ANNUAL TEMPERATURE
ANNUAL TEMPERATURE RANGE
ACTUAL EVAPORATION
MEAN ANNUAL RAINFALL
RANGE IN RAINFALL
WATER SURPLUS
MDC
MDC
B
A
CCA & LNR REGR.
CAPSULE
POD
DRUPE
BERRY
NUT
ALL FRUIT TYPES
MDC
WHITE
RED
ORANGE
YELLOW
GREEN
BROWN
BLACK/BLUE
FRUIT COLOUR
<15 mm
15 - 30 mm
>30 mm
SIZE

represented. The unshaded arrows (A) represent results derived from the environment/fruit type/size [FE, FS] model, whereas shaded arrows (B) indicate the environment/fruit type/colour [FE, FC] model defined at a 95% goodness of fit. These relationships are uni-directional since the environmental variables may be hypothesized as "causal" and the fruit types a "response".

It must be stressed that these relationships represent hypotheses only, since no causality can be inferred from statistical analyses, even though the data for the MCD are modelled on an assumption of causality to determine the relative goodness of fit between different models. Intensive and individual studies are now required to test the validity of each of these relationships.

Biotic implications of these hypothetical relationships

The hypothesized speciation of pod-bearing species (which mostly belong to the Leguminosae) under conditions of hot mean temperatures and areas of low altitude ranges tends to confine this group to the central Kalahari plateau. This speciation may also be related to the distribution of antelope which may consume the hard pods and disperse the seeds (van der Pijl 1969; Lamprey _et al_. 1974). The hard dry seeds, although an adaptation to resist strong molars may function to limit desiccation, and make this seed type suitable to arid areas.

The drupe fruits are usually associated with bird and mammal dispersal in mesic non-seasonal forests where the single seed is an adaptation for the seedling which must wait for an opening in the forest canopy before growth can take place. The hypothesised speciation of these fruit types under conditions of water shortage and high solar radiation may possibly be attributed to large seeds being preadapted to such conditions. A large seed may (a) possess a hard seed testa that possibly reduces excessive desiccation and (b) supply the seedling with a food source under conditions that may otherwise prevent the uptake of nutrients from the substrate.

Berry species are usually considered to be bird and mammal dispersed and to occur in areas of open and secondary vegetation, when a large number of seeds of a smaller size may be an adaptation to maximize dispersal to vacant spaces. The hypothesized speciation under conditions of high mean annual rainfall which characterize eastern sectors of the subcontinent would seem, however, to indicate that the small seeds are not suitable for dispersal in arid areas, even though many vacant spaces may be present.

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PART 4

DISTRIBUTION AND EVOLUTION OF ARIL-BEARING TREES IN SOUTHERN AFRICA

ABSTRACT

The spatial distribution of the indigenous southern African aril-bearing tree flora (70 species) is analysed, to determine patterns of species similarity and environmental dependence. Six geographical regions are identified, but differences in species composition between the regions are relatively small. There is no evidence for an east-west dichotomy in the species composition of the flora, concomitant with a rainfall gradient. Proportional species richness (the percentage of aril-bearing species in the total indigenous tree flora), however, is highest in the dry western sectors of the subcontinent. Correlations with rainfall, temperature, solar radiation, altitude and water surplus, suggest that the aril-bearing species are environmentally tolerant and are capable of occupying expansive geographical ranges. Fruiting periods tend to be short in individual species, but fruit is available throughout the year in four regions. These results are discussed in relation to hypotheses for the evolution of the aril-bearing flora.

INTRODUCTION

Plant species which rely on animals for seed dispersal usually produce fruits which are fleshy and derived from drupe, berry or arillate morphologies (Snow 1971). These fruits are most often conspicuous or possess strong scent to attract the appropriate dispersal agents, while the premature exploitation of these fruits is prevented by either the presence of toxin and/or inconspicuous colouration of the unripe berry or drupe or by an enclosed capsule or pod in the case of the arillate fruits. The arillate fruits are often considered to be particularly important sources of food for birds (Skutch 1980, Snow 1981) and mammals (Howe 1980), even though species possessing such fruits constitute only approximately 10% of the total humid tropical tree flora bearing ediable fruits (Corner 1949). Based on the arillate fruits of the Durio zibethinus, the Durian theory of Corner (1949) assumes "the primitive angiosperm fruit must have been a red fleshy follicle, probably spiny, with large black seeds hanging on persistent funicles and covered with a red aril" and to have existed in the mesophytic tropical conditions.

Axelrod (1952, 1960) postulated that such conditions stimulated the evolution and spread of the angiosperms. The fleshy multicarpellate fruits produced by certain tropical members of the Magnoliaceae have also been proposed as a primitive form of reproduction in angiosperm trees (Takhtajan 1969). Although species producing carpel fruits may have given rise to many modern forms producing berries and drupes, the aril-bearing tree species occur in some 45 extant families (Corner 1949), of which 29 occur in southern Africa, and 31 are predominantly tree or woody plant species (Heywood 1978).

The modern arillate fruit is thought to represent a compromise between a juicy non-dormant sarcotest and the requirements for dormancy and hardening which should favour aril-producing species in areas outside humid forests (Van der Pijl 1969). The following is a report on an analysis of the gross spatial distribution of the indigenous southern African aril-bearing tree flora, comprising 70 species, in relation to suites of environmental features which might influence the dispersion of the flora. This permits a discussion of aspects of the possible origin and evolution of the flora and the modern arillate fruit in the light of the Durian theory.

MATERIALS AND METHODS

The main data base on 70 species of indigenous aril-bearing tree species (Appendix 2) occuring in southern Africa was assembled from maps in Coates Palgrave (1977). These maps are the only published source of this imformation, and represent generalized distributions only, and therefore a coarse grid of seventy quadrats was employed (Fig. 1). Each quadrat was scored for each species according to a 1-10 scale, with each of the 10 numerials accounting for 10% of the area of each quadrat. The proportional criteria for data transformation eliminates the requirement of equal area quadrats (Knight _et al._ 1982).

Cluster analysis based on a Bray-Curtis similarity coefficient and group-average sorting (Field & McFarlane 1968), together with multi-dimensional scaling (Kruskal 1964) were used to identify groups of quadrats with similar species compositions. Information statistic tests (Field 1969) were used to determine the species which characterized the groups of quadrats. Proportional species richness (defined as the percentage of aril-bearing species in the total indigenous tree flora) was related to 12 measures of the environment through correlation and stepwise multiple linear regression analyses (Sokal & Rohlf 1969; Allen 1973). The measures of the environment are:-

Solar radiation - mean annual (XSR)
annual range (RSR)
Temperature - mean annual (XT)
mean annual range (XTR)
January maximum (JAMA)
July minimum (JUMI)
Rainfall - mean annual (XRF)
mean January (JARF)
mean July (JURF)
Altitude - range (RA)
Water Surplus - rainfall minus evaporation (WP)

The environmental data were taken from Talbot & Talbot (1960), Jackson (1961), Thornthwaite (1962), Clark (1967), and Schulze & McGree (1978). Proportional species richness is not a continuous variable and, therefore, was converted to a squared arcsine function (Fisher & Yates 1963). The proportional species richness for each quadrat was subjected to a contouring program (S.G.P. Diederiks 1979) which fitted a two-dimensional contour surface, by a least squares polynomial analysis. The proportional species richness was further analysed for spatial dependence (or randomness) in preset directions through spatial autocorrelation (Cliff & Ord 1969 1973; Ward 1978). The fruit seasons for each species within each region (identified by the cluster analysis) together with the mean length of all the species fruiting seasons within the regions were determined from information in Coates Palgrave (1978). These methods were used to determine if a continuous supply of fruit was available in each region.

RESULTS

Aril-bearing tree species clustered into five regions: (A) Bushveld; (B) Northern Namib; (C) Mozambique Coastal; (D) Arid Karoo; and, (E) Subtropical Coastal (Figs 7 & 8). Also present is a fragmentary Karoo Periphery (F). Among the species characteristic of each region, those belonging to *Commiphora* and *Maytenus* predominate in the Bushveld and Subtropical Coastal regions, respectively (Appendix 2). The spatial pattern displayed by the aril-bearing species is simpler than that of the total tree flora (cf. Figs 8 & 9).

There is no evidence for an east-west dichotomy in the species composition of the aril-bearing flora, concomitant with a rainfall gradient. An ordination plot for species similarity among the 70 quadrats, over which is superimposed the 400 mm isohyet (a line which almost divides the subcontinent into moist eastern and dry western sectors), bisects the Bushveld (A) and the Arid Karoo (D) (Fig. 10). Both of these regions are characterized by a moderately large number of aril-bearing species (Appendix 2). The two dimensional contour map (Fig. 11) indicates that the highest proportional species richness of the aril-bearing flora occurs in the dry western parts of the sub-continent. The proportional species richness (TARIL) is correlated negatively, and most strongly, with mean annual rainfall (r = -0,792, P < 0,01) and

Fig. 7. Dendrogram formed by the Bray-Curtis similarity coefficient and group-average sorting (Field & McFarlane 1968) of the southern African aril-bearing tree flora. Regions A-F are identified at a 25% similarity level.

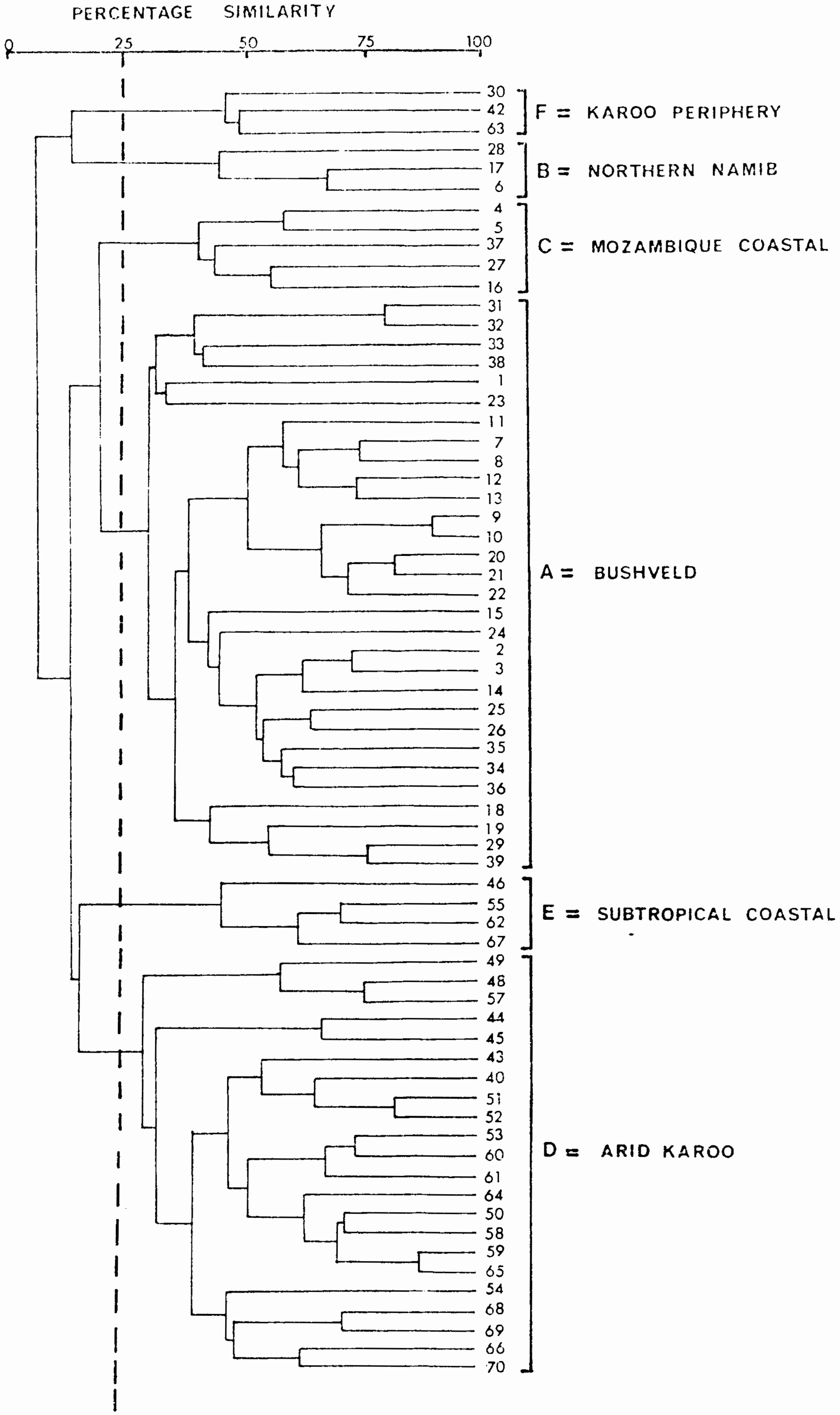

PERCENTAGE SIMILARITY
0
25
50
75
100
30
42
63
F = KAROO PERIPHERY
28
17
6
B = NORTHERN NAMIB
4
5
37
27
16
C = MOZAMBIQUE COASTAL
31
32
33
38
1
23
11
7
8
12
13
9
10
20
21
22
15
24
2
3
14
25
26
35
34
36
18
19
29
39
A = BUSHVELD
46
55
62
67
E = SUBTROPICAL COASTAL
49
48
57
44
45
43
40
51
52
53
60
61
64
50
58
59
65
54
68
69
66
70
D = ARID KAROO

Fig. 8. Cartographic representation of the southern African aril-bearing tree flora, based on cluster analysis. Names of regions A - F are given in Fig. 7. Hatched quadrats indicate a lack of data.

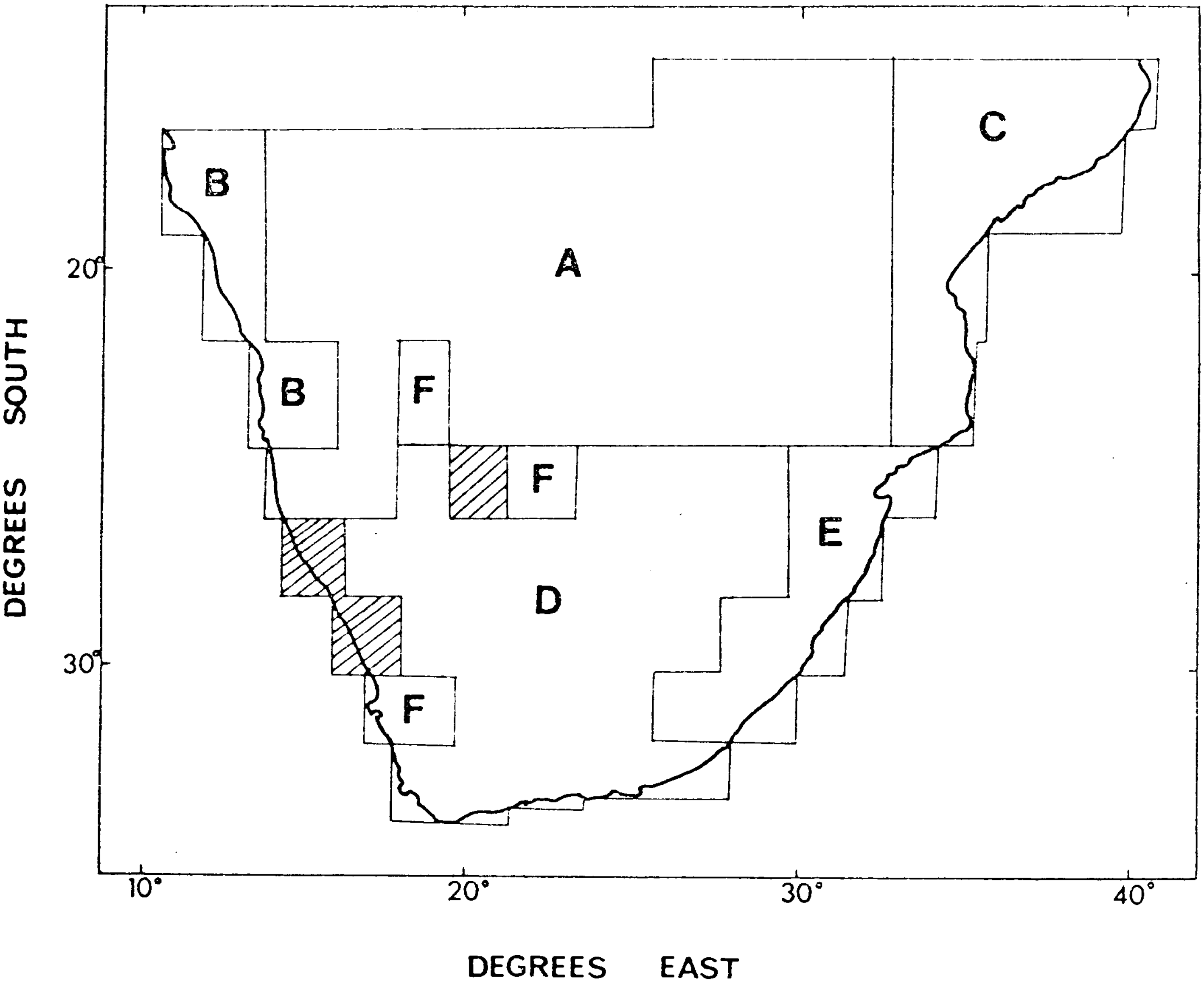

A
B
B
C
D
E
F
F
F
20°
30°
10°
20°
30°
40°
DEGREES SOUTH
DEGREES EAST

Fig. 9. Cartographic representation of the total southern African tree flora (1 362 species), based on information in Knight *et al.* (1982). Names of regions (identified at a 25% similarity level) are: B = Northern Namib, D = Arid Karoo, G = Eastern Bushveld, H = Western Bushveld, I = Afromontane, J = Kalahari, K = South Central Namib and L = West Coast Karoo.

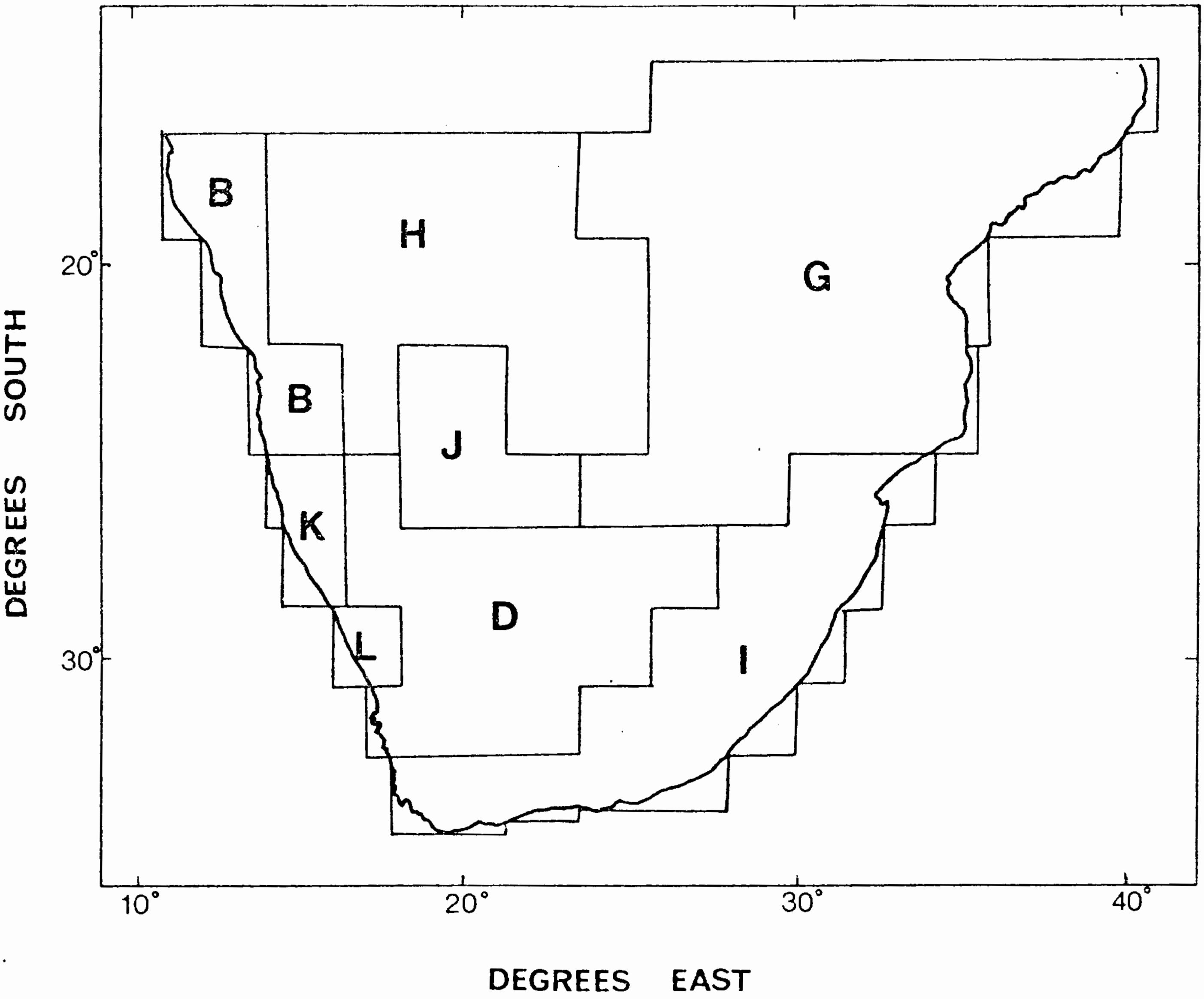

B
H
G
B
J
K
D
L
I
20°
30°
10°
20°
30°
40°
DEGREES SOUTH
DEGREES EAST

Fig. 10. Multi-dimensional scaling ordination of the southern African aril-bearing tree flora. The diagonal represents the 400mm isohyet. Positions of individual quadrats (indicated by numbers) are shown in Fig. 1. Names of regions A - F are given in Fig. 7.

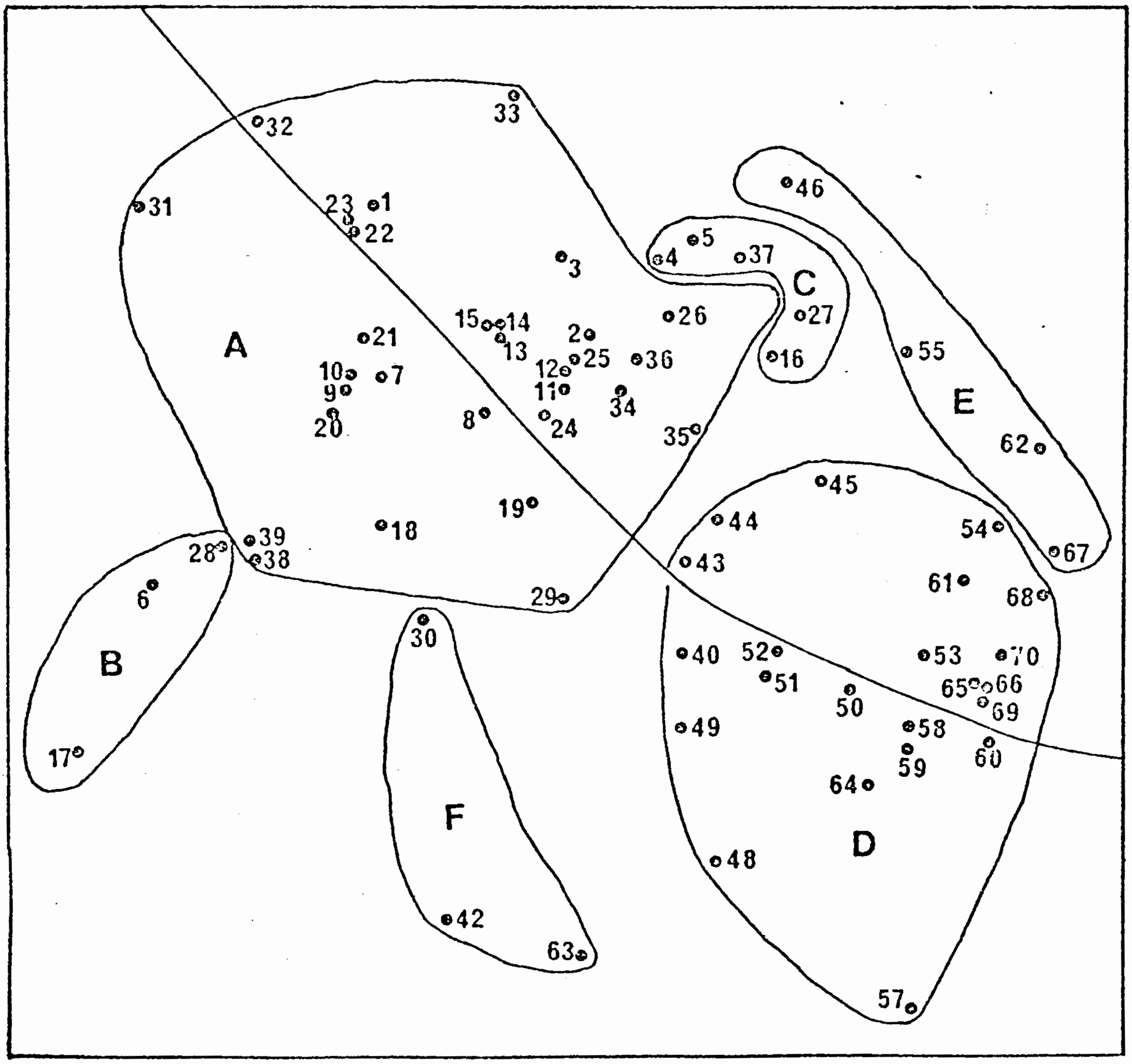
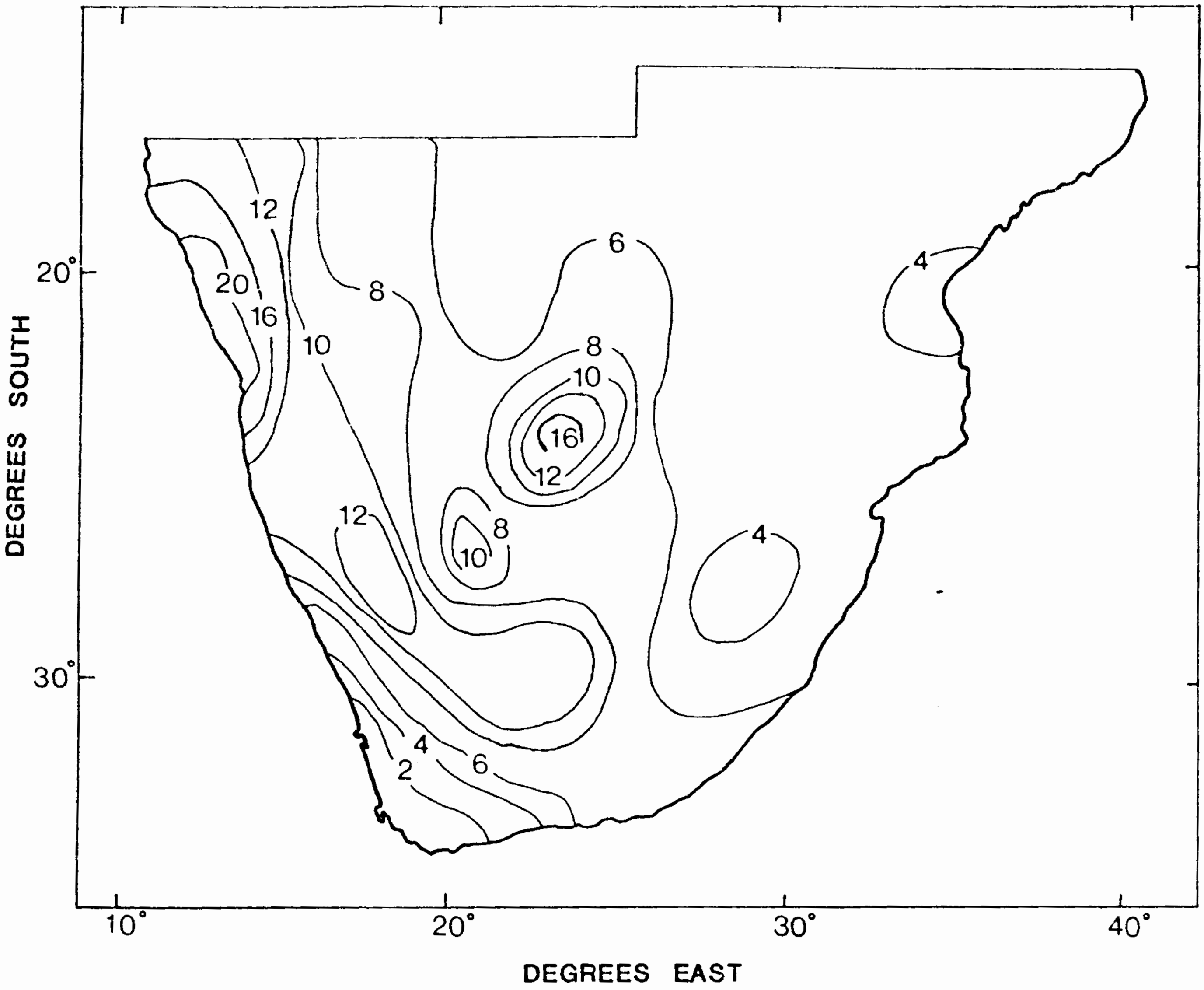

32
33
46
31
23
1
22
5
4
37
3
C
15
14
2
26
27
A
21
13
25
36
16
55
10
7
12
9
11
34
E
8
20
24
35
62
45
19
44
54
39
18
67
28
38
43
61
6
29
68
30
B
40
52
53
70
51
65
66
50
69
58
49
60
17
59
64
F
48
D
42
63
57

Fig. 11. Two-dimensional contour map of proportional species richness of the southern African aril-bearing tree flora. All numbers are percentages.


12
6
4
20
8
16
10
8
10
16
12
12
8
10
4
4
6
2
20°
30°
10°
20°
30°
40°
DEGREES SOUTH
DEGREES EAST

July (winter) rainfall (r = -0,310, P < 0,01), but positively with mean solar radiation (r = 0,335, P < 0,01) (Table 18). The above rainfall variables and range in solar radiation are the only variables included in the regression equation (Table 19), which has a low coefficient of determination (R^2 = 0,18, 0,25 and 0,32 for the successive inclusion of XRF, JURF, and RSR in the regression equation), suggesting that the distribution of the aril-bearing flora cannot be determined, in statistical terms, from the environmental features considered here. This also suggests that the aril-bearing tree species, as a group, are environmentally tolerant and are capable of occupying relatively expansive geographical ranges. Results of spatial autocorrelation for proportional species richness of the southern African aril-bearing tree flora indicate that the pattern is spatially dependent in N-S (z = 3,70, P < 0,01) and NW-SE directions (z = 3,44, P < 0,01), but is random for NE-SW (z = 0,11, n.s.); the latter probably reflecting an impoverished aril-bearing flora in the south-western Cape corner of the subcontinent (Table 20). These results are reflected in the contour map of proportional species richness (Fig. 11). The fruiting periods of the aril-bearing species are relatively short (Table 21). In four of the five regions, however, there is a continuous, but uneven, supply of fruits almost throughout the year (Fig. 12). This suggests that shifts in the seasonal production of fruit along gradients from temperate to subtropical zones are lacking, and probably reflects the absence of migrations along such routes by frugivorous birds in southern Africa.

DISCUSSION

If aril-bearing species generally represent "primitive"

TABLE 18 Correlation coefficient matrix of proportional species richness of 70 aril-bearing tree species (TARIL) and 12 measures of the environment

	Solar Radiation		Temperature				Rainfall					
	Mean annual (XSR)	Annual range (RSR)	Mean annual (XT)	Mean annual range (XTR)	January max. (JAMA)	July min. (JUMI)	Mean annual (XRF)	Mean annual range (RRF)	Mean January (JARF)	Mean July (JURF)	Altitude range (RA)	Water surplus (WP)
RSR	-0,057											
XT	-0,463	-0,157										
XTR	0,496	-0,078	-0,062									
JAMA	0,098	-0,177	0,455	0,612								
JUMI	-0,347	0,008	0,421	-0,752	-0,269							
XRF	-0,792	0,191	0,181	-0,378	-0,126	0,138						
RRF	-0,394	-0,067	0,029	-0,446	-0,102	0,288	0,627					
JARF	-0,472	-0,068	0,246	-0,185	0,080	0,152	0,431	0,225				
JURF	0,117	0,015	-0,271	-0,143	-0,418	0,102	0,121	0,243	-0,136			
RA	-0,165	0,208	-0,441	-0,486	-0,550	0,089	0,336	0,415	-0,057	0,445		
WP	-0,470	0,057	0,157	-0,454	-0,013	0,275	0,542	0,481	0,316	0,070	0,345	
TARIL	0,335	0,171	-0,205	0,063	-0,035	-0,040	-0,427	-0,303	-0,241	-0,310	-0,184	-0,236

Critical values of *r* for significance levels are: *r*=0,237 *P*=0,05; *r*=0,309 *P*=0,01; *r*=0,388 *P*=0,001.

Table 19. Results of stepwise regression analysis between proportional species richness of the southern African aril-bearing tree flora and the environmental variables listed in Table 18.

	Coefficient of determination (R^2)	Regression coefficient (Z)
Rainfall Mean annual (XSR)	0,18	-0,0001
Rainfall Mean July (JURF)	0,25	-0,0017
Solar Radiation Annual range (RSR)	0,32	-0,0024

Table 20. Results of spatial autocorrelation for proportional species richness of the southern African aril-bearing tree flora.

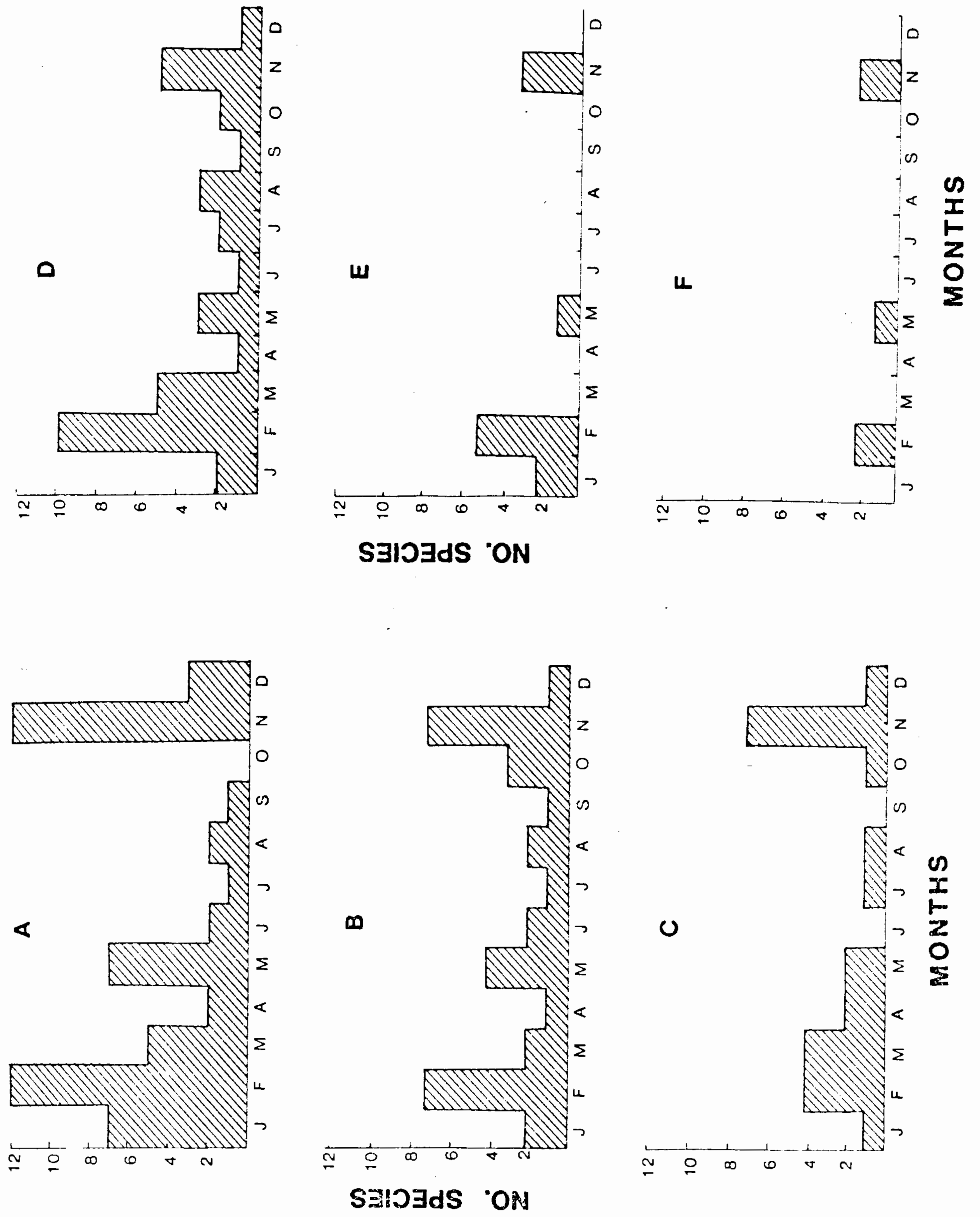
Direction	Joints	Autocorrelation (*r*)	Absolute value (*z*)
N-S	116	0,46	3,70
E-W	120	0,30	2,55
NW-SE	108	0,44	3,44
NE-SW	110	0,00	0,11
OVERALL	454	0,30	5,13

Critical values of z for significance levels are : z = 2,00 P = 0,05; z = 3,00, P = 0,01 (Ward 1978)

Table 21. Mean duration (months) of fruit presention of species bearing arillate fruits in six regions of southern Africa

Region	No. species	Fruiting duration	Coefficient of variation
Bushveld (A)	54	3,36	53 %
N. Namib (B)	33	4,03	47 %
Mozambique C. (C)	24	3,79	28 %
Arid Karoo (D)	36	4,08	56 %
Subtropical C. (E)	12	2,73	33 %
Karoo P. (F)	5	3,60	50 %

Fig. 12. Number of aril-bearing tree species presenting fruit according to months and regions in southern Africa. Names of regions A - F are given in Fig. 7.


A
B
C
D
E
F
NO. SPECIES
NO. SPECIES
MONTHS
MONTHS
12
10
8
6
4
2
J
F
M
A
M
J
J
A
S
O
N
D

angiosperm trees which originated in the humid tropics, as suggested by Corner (1949), then a greater degree of dependence on environmental conditions, particularly rainfall, than has been demonstrated here could have been anticipated. Indeed, it appears that there is no dichotomy in the species composition of the southern African aril-bearing tree flora, concomitant with a rainfall gradient, and that species richness is proportionately highest in the dry western parts of the subcontinent. The potential environmental determinants used explain only 32% of the distribution of this flora, in contrast to 63% in a comparable study based on all (n = 1 362) tree species in southern Africa (Knight _et al._ 1982). Moreover, at least three geographical refugia for relict species were found for this entire tree flora (Knight _et al._ 1982), whereas the aril-bearing species tend to have very wide distributional ranges with no centres of isolation. Thus, the southern African aril-bearing tree flora might have evolved under semi-arid conditions, as suggested for the angiosperms generally (Stebbins 1971), and subsequently invaded mesic regions.

Animal dispersers either accompanied the plants, or relationships with new dispersal agents had to be formed in the mesic regions. The humid tropics are believed to be centres for the evolution of frugivory (Corner 1949; Van der Pijl 1969) and, therefore, a relative abundance of potential biotic dispersers could have been available to the plants in their new environment. It seems reasonable to assume that, aril-producing species would have encountered fewer opportunities for establishing relationships with animal dispersers in spreading from mesic to xeric areas. Many southern African arillate fruits are nutritionally rich and have large seed: pulp ratios (P.G. Frost pers. comm., pers. obs). According to McKey (1975), species producing such fruits tend to be dispersed by obligate frugivores and, being specialists rather than opportunists, they are unlikely to pioneer ecologically new areas, as would be the case if they evolved in humid habitats and subsequently moved into arid regions.

Assuming that aril-producing species tend to have a specialist dispersal mode (McKey 1975), then, selection should favour temporal displacement of fruiting periods in sympatric species producing fruits containing similar nutrients. Since most of southern Africa is extratropical, pronounced seasonality in climate is the norm and this probably promotes seasonal peaks in fruit presentation (cf. Liversidge 1972), and militates against a high degree of displacement of fruiting periods (Leck 1972). Nevertheless, fruiting periods in the aril-bearing tree flora are displaced to some extent, providing a continuous, but uneven, supply of fruit throughout the year in most regions. McKey (1975) also predicted that, in species which produce fruits with nutritious pericarps, fruiting periods should last a long time and that individual fruits should be displayed for a long time on the tree. Fruiting periods are, however, not markedly long in the southern African aril-producing tree flora, possibly reflecting a relatively high incidence of species producing low quality fruits at low cost. This might apply to members of Commiphora whose fruits, similarly to the seeds of Erythrina (Krukoff 1969), could also be mimics of more nutritious arillate fruits. Since there are at least 33 species of Commiphora in southern Africa, their abundance is likely to supersaturate the species being mimicked.

In general, these findings prompt caution in the use of "opportunist" (or "generalist") and "specialist" when discussing the evolution of fruit types. It seems likely that more species than not occupy places somewhere on an axis between these two extreme positions, and that each species has a degree of flexibility for movement along part of the axis in response to proximate factors, in addition to ultimate evolutionary shifts.

Finally, an alternative hypothesis involves neither a mesic to xeric nor a xeric to mesic shift in the primary spread of the aril-bearing tree flora of southern Africa. Forest formerly extended over considerably greater areas of the subcontinent, under the influence of a southerly extension of the tropical rainfall system during interglacial periods (Van Zinderen Bakker 1969). Aridity prevailed over most of the area during the intervening periods, causing the forest to become fragmented and restricted to refugia (Van Zinderen Bakker 1969). Aril-bearing species may, however, have been relatively well equipped, or pre-adapted (e.g. dry fruit, hard seed coat for dormancy), for dry conditions and, thus, remained behind while the forest retreated. In this way, a fairly constant similarity in species composition of the aril-producing tree flora could have arisen over large areas of the subcontinent, with proportional species richness varying due to the disproportional retreat of species less tolerant of arid conditions.

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PART 5

THE BIOGEOGRAPHICAL AND EVOLUTION OF FRUIT/FRUGIVORE RELATIONSHIPS IN SOUTHERN AFRICA

ABSTRACT

The southern African frugivorous avifauna is divided into two classes; species that specialize on a fruit diet and species that include fruit in their diet on an opportunistic basis. The spatial distribution of these two classes of avian frugivores are analysed to determine the patterns of species similarity. Within each region identified for the two avifauna groups; frequencies of characterized plant species possessing fleshy fruits are determined together with fruit size and seasonal availability. The relationship of frugivorous birds with these plant species does not appear to change markedly with latitudinal changes, although such relationships do change with increasing aridity.

INTRODUCTION

Theoretical models on evolutionary relationships between frugivorous birds and their food plants predicts a dichotomy of strategies characterized at one extreme by a specialized frugivore that feeds on a high quality fruit (protein and lipid rich) while the other extreme is represented by an unspecialized frugivore that feeds on less nutritious fruits providing a carbohydrate rich supply (McKey, 1975). From this premise it has been suggested that specialized rich fruit-based systems equivalent to Howe & Estabrook's (1977) model 1 are particularly common in the tropics as opposed to temperate habitats where environmental restraints produce poor-fruit based plant-bird systems (model 2) (Snow, 1971; Morton, 1973). The fruits of model 1 (Howe & Estabrook, 1977) are typically large, containing few relatively large seeds and may be drupaceous or arillate. Fruits associated with model 2 are typically smaller and contain many small seeds (McKey, 1975; Snow, 1976, 1981). The fruiting phenology of plants associated with these two models are also distinctive. Model 1 fruiting should be spread out over a relatively long period, while selection by the frugivores may favour the spread and overlap of fruiting seasons of fruit supplying different nutrients, and a constant supply of fruits throughout the year is maintained. In model 2 selective pressures should favour the supply of fruit when other food resources are in short supply (e.g. invertebrates and graminaceous fruits) and thus a short fruiting season may be expected.

The testing of these predictions requires a detailed knowledge on fruit structure, morphology and chemical composition, together with detailed observations on the frugivores that disperse them.

This information is required for a large number of plants and on a continental scale. Some indications, however, may be derived if a population of selected species (in this case trees or woody plants) are used together with a broad assumption that fruits with a 'berry' morphology will have smaller seed sizes and will thus fall into a model 2 dispersal, while the 'drupe' morphology characterized by a single but relatively larger seed size would be better represented as a model 1 dispersal.

Depending on the validity of these assumptions the following predictions may be anticipated:-

(1) Subtropical areas (e.g. Mozambique coast) should be represented by a greater number of drupe-bearing species (model 1), while the more temperate areas (e.g. S.W. Cape) should have a greater representation of berry (model 2) fruits.
(2) In the subtropical areas, drupaceous fruits (model 1) should be characteristically large, while both drupe and berry fruits may be expected to be smaller in the temperate areas.
(3) The subtropical areas should be represented by a more continuous fruit supply, with each species possesing a longer fruiting season than the temperate areas.
(4) The specialist frugivores should be less numerous, but on a proportional basis be better represented in the subtropical areas, and have restricted geographical distributions.
(5) Opportunist frugivores should have wider geographical distributions and a larger representation over the more temperate regions of southern Africa.

METHODS

Data extraction

Data on plant distribution were extracted from Coates Palgrave (1977) while information on fruit size, morphology (berry/drupe) and fruiting season were extracted from Palmer & Pitman (1972 & 1973), van Wyk (1972-1974), Palmer (1977), Coates Palgrave (1977) and Moll (1981).

The distributional data for birds was taken from Hall & Moreau (1970) and Snow (1978). The frugivorous birds were partitioned into those specializing in a fruit diet for the greater part of their life cycle and those avian species that eat fruit on an opportunistic basis (Appendix 3). These divisions although subjective were based on information in McLachlan & Liversidge (1978), Rowan (1970) and food/diet studies based at the FitzPatrick Institute.

Analytical techniques

A seventy quadrat grid was used to transform each distribution map of frugivorous birds into a numerical form (Fig. 1). Cluster analysis, multidimensional scaling, ordination and information statistics tests were used to define areas with similar species assemblages for both the specialist and opportunist bird populations. These techniques are described more fully in Knight _et al._ (1982). The seasonal availability of fruit of a model 1 dispersal (drupe) and model 2 (berry) fruit for the regions defined by both avian dispersal classes were plotted together, as were the categories of fruit size (mm). The breeding season of opportunist and specialist avian species was also plotted from data taken from MacLachlan & Liversidge (1978).

RESULTS

Species similarity patterns

Cluster analysis results of specialist and opportunist frugivores are represented as a paired dendrogram (Fig. 13). Two similarity levels were selected by inspection at 35% and 45% levels. It may be noted that more provinces are recognized for the opportunist frugivores than the specialized frugivore, and further in several provinces more divisions at a subprovince level have occurred (cf. Figs 14a & 14b). This implies that those species feeding on fruit opportunistically have narrower geographical ranges/distributions than the specialist frugivores. Fragmentation of provinces and subprovinces has occurred in the central (Kalahari) plateau areas in both avian populations.

The specialist frugivorous birds have divided into a tropical-temperate dichotomy along the south and east coastal belts (Fig. 16). Region B1 represents the tropical and subtropical fauna, while region A1 represents the temperate fauna. Regions A2 and B2 probably represent the transitions between these two faunal groups. Interestingly the temperate fauna moves inland when approaching the subtropics, where altitude may ameliorate the temperature conditions. In the western areas, however, no tropical-temperate dichotomy occurs (e.g. subprovince C1 expands across nearly all possible latitudes). This probably represents a paucity of fruit-eating species existing in the arid areas (e.g. no statistically characterized species occurred in F1 and thus such a region is a consequence of the numerical analyses). When a tropical-temperate latitude line (23° S lat.) is drawn across ordination plots (Figs 15 & 16) only the opportunist frugivore indicate any dichotomy, this probably reflects the total non-existence of any dichotomy in arid areas of the specialist frugivores, and that environmental factors are more important than latitudinal factors *per se*. This line drawn on the opportunist

Fig. 13. A paired dendrogram formed by the Bray-Curtis (1957) similarity coefficient and group average sorting (Field & McFarlane 1968) for southern African specialist (left) and opportunist avian frugivores. The names of the regions identified at the 45% similarity level are: A1 = Southern Afromontane, A2 = Northern Afromontane, A3 = Zimbabwe Northern Bushveld, B1 = Bushveld, B2 = Southern Coastal Bushveld, B3 = Mozambique Bushveld, C1 = Arid Karoo, C2 = Karoo-South Namib, C3 = Karoo-Kalahari, C4 = Karoo-Bushveld, D1 = Combretum Savanna/Bushveld, D2 = Acacia Bushveld, D3 = Northern Namib, E = West Coast Karoo, F1 = S.W.A. /Namibian Kalahari, F2 = Peripherial Kalahari.

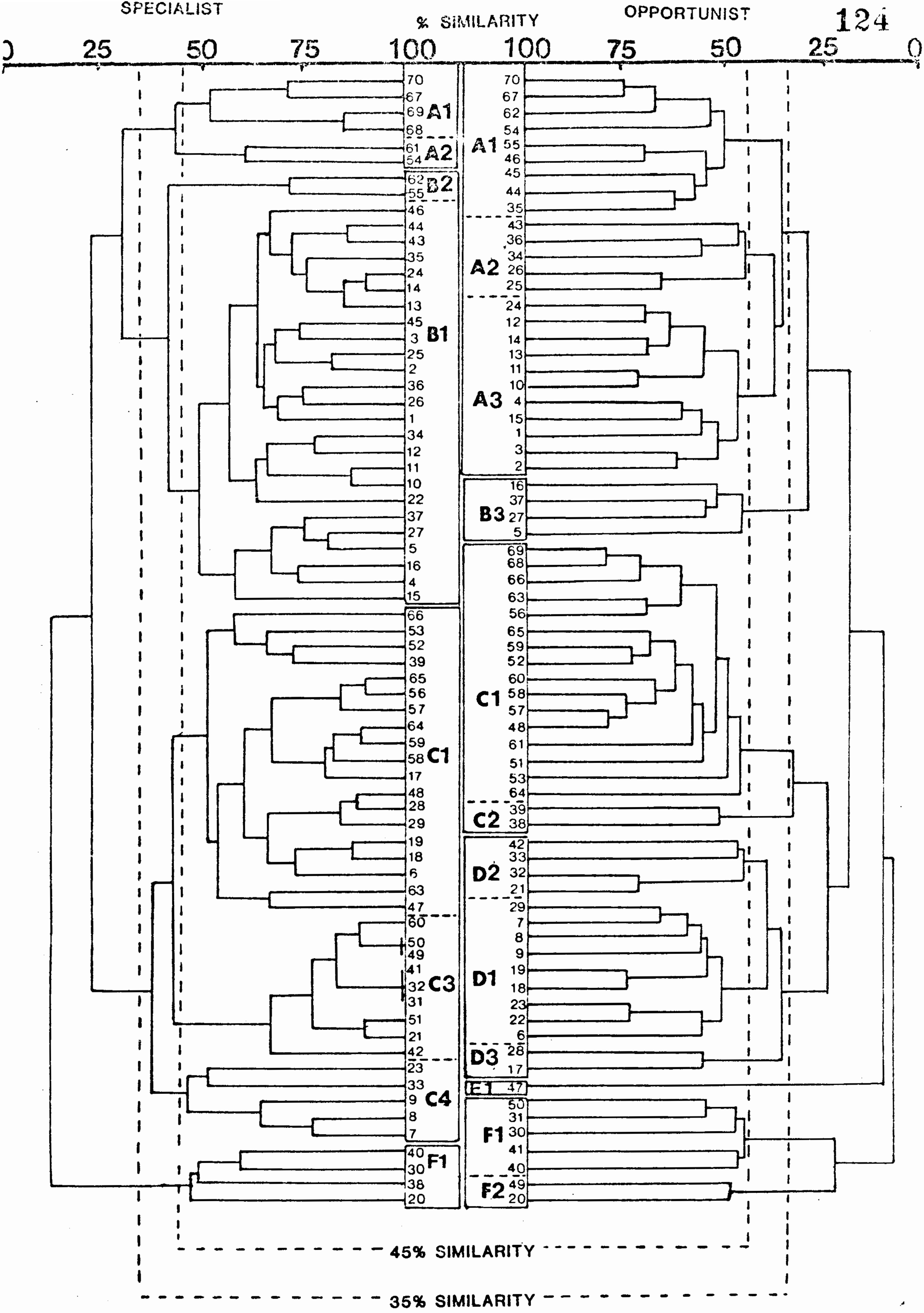
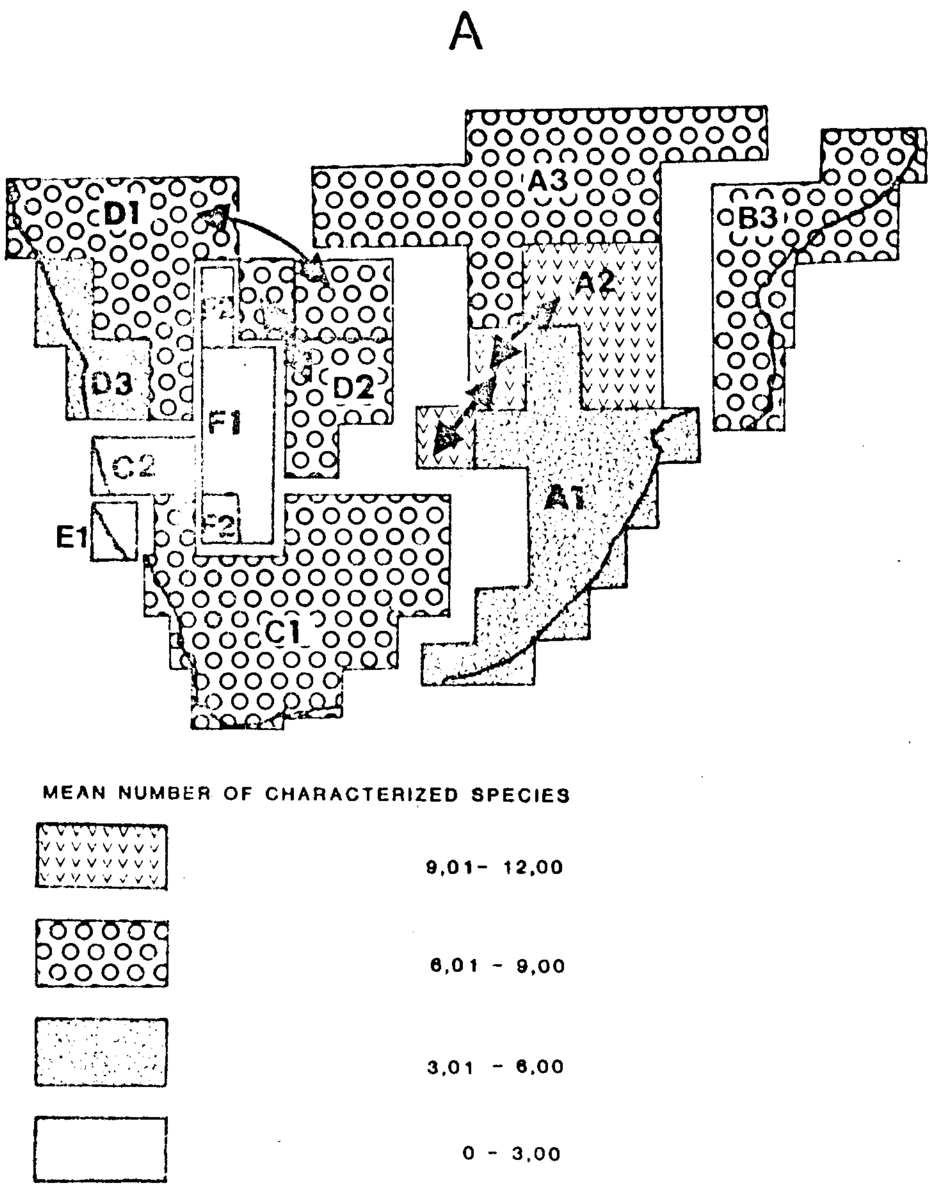

SPECIALIST
% SIMILARITY
OPPORTUNIST
0
25
50
75
100
100
75
50
25
0
A1
70 67 69 68
A2
61 54
B2
62 55
B1
46 44 43 35 24 14 13 45 3 25 2 36 26 1 34 12 11 10 22 37 27 5 16 4 15
C1
66 53 52 39 65 56 57 64 59 58 17 48 28 29 19 18 6 63 47
C3
60 50 49 41 32 31 51 21 42
C4
23 33 9 8 7
F1
40 30 38 20
A1
70 67 62 54 55 46 45 44 35
A2
43 36 34 26 25
A3
24 12 14 13 11 10 4 15 1 3 2
B3
16 37 27 5
C1
69 68 66 63 56 65 59 52 60 58 57 48 61 51 53 64
C2
39 38
D2
42 33 32 21
D1
29 7 8 9 19 18 23 22 6
D3
28 17
E1
47
F1
50 31 30 41 40
F2
49 20
45% SIMILARITY
35% SIMILARITY

Fig. 14. Cartographic representation of the opportunist frugivore dendrogram (a) and the specialist frugivore dendrogram (b). The region names are listed in Fig. 13. The shading indicates the mean number of species characterized by information statistics tests per region.


A
D1
A3
B3
A2
D3
D2
F1
C2
A1
E1
F2
C1
MEAN NUMBER OF CHARACTERIZED SPECIES
9,01- 12,00
6,01 - 9,00
3,01 - 6,00
0 - 3,00

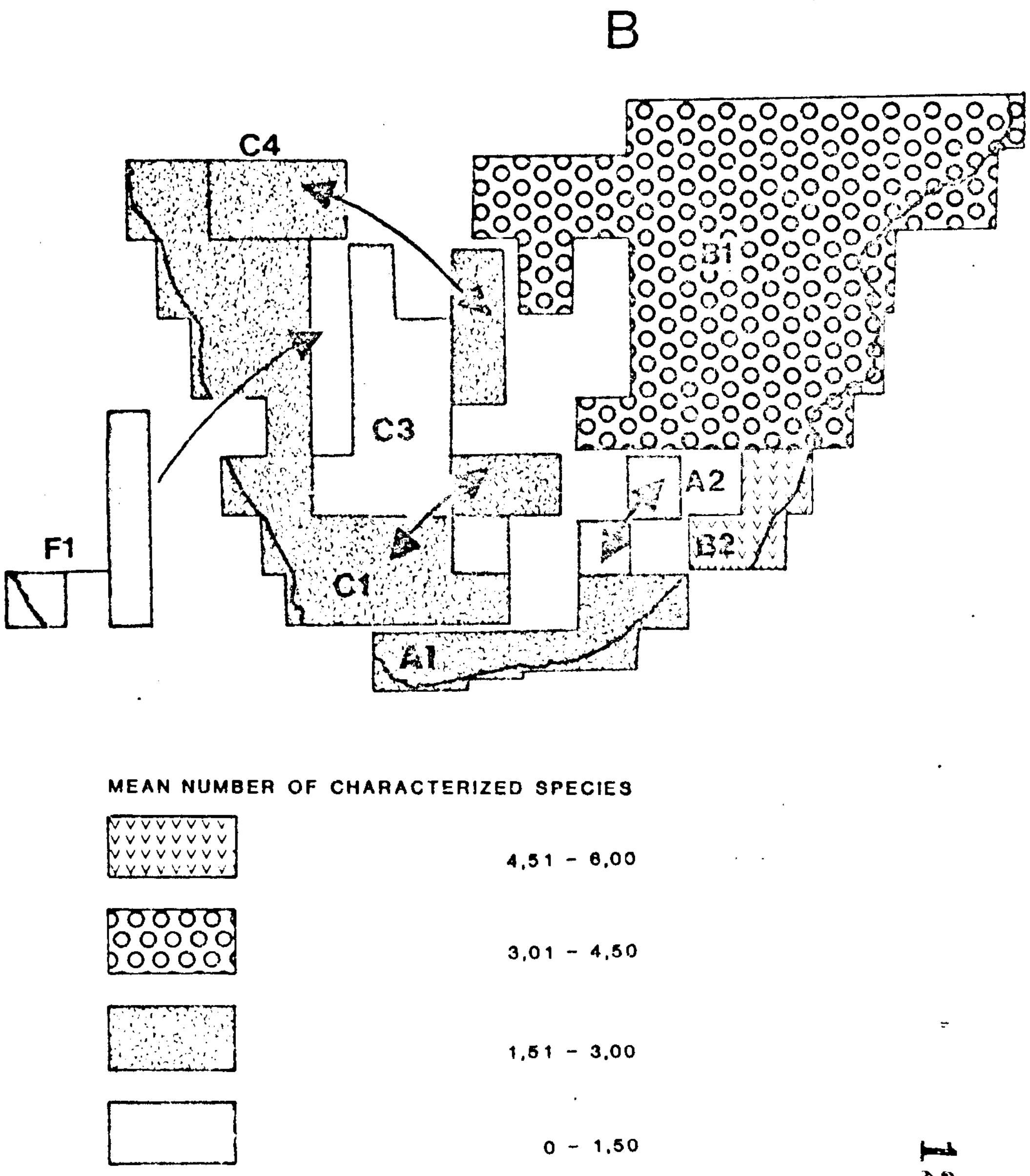

B
C4
B1
C3
A2
F1
B2
C1
A1
MEAN NUMBER OF CHARACTERIZED SPECIES
4,51 - 6,00
3,01 - 4,50
1,51 - 3,00
0 - 1,50

Fig. 15. Multi-dimensional scaling ordination of the southern African opportunistfrugivore avifauna. The double line represents the 400 mm isohyet, while the dotted double line represents the 23° S lat. The region names are listed in Fig. 13. Position of individual quadrats (indicated by numbers) are given in Fig. 13.

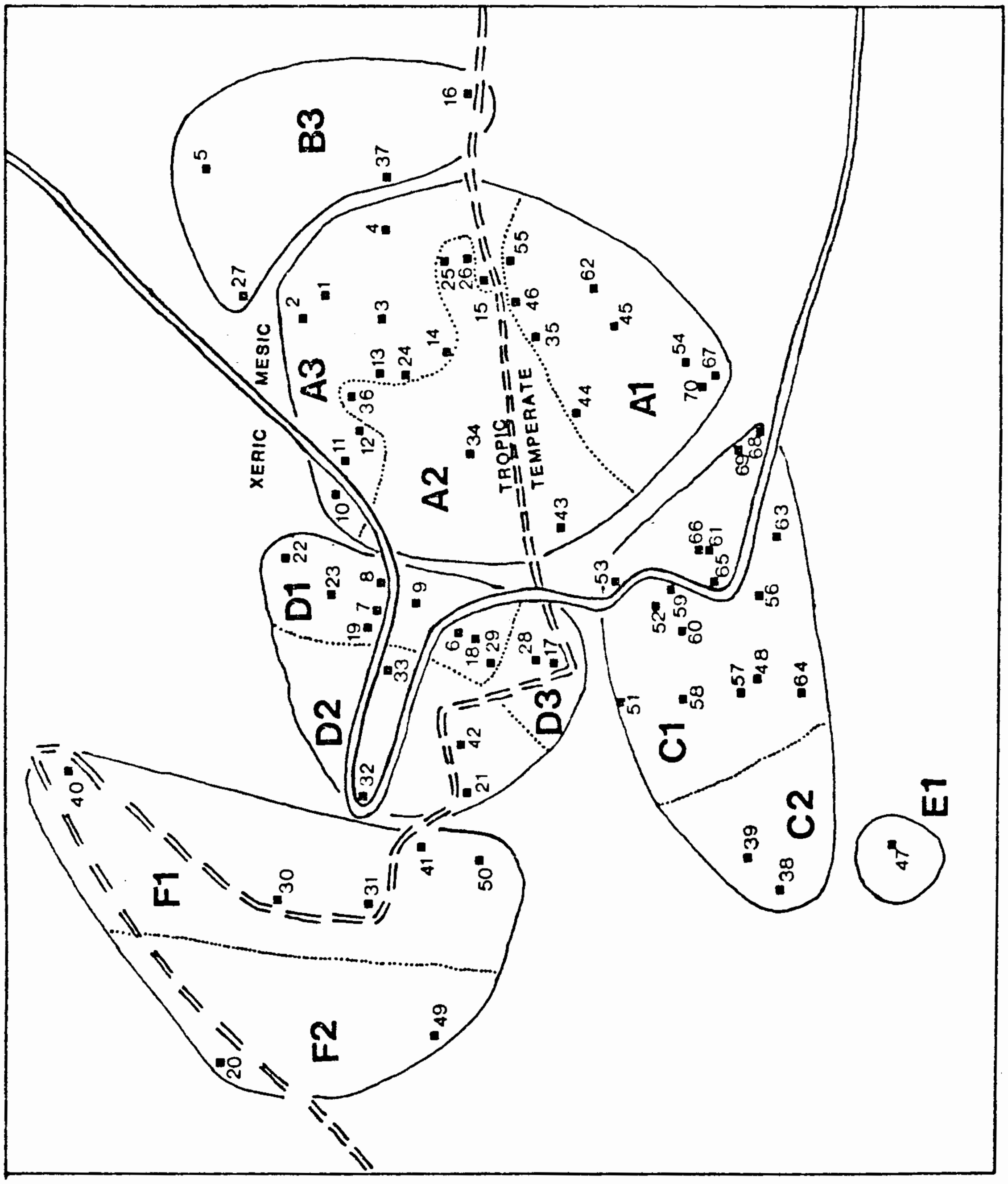

B3
A1
A2
A3
D1
D2
D3
C1
C2
E1
F1
F2
XERIC
MESIC
TROPIC
TEMPERATE
1
2
3
4
5
6
7
8
9
10
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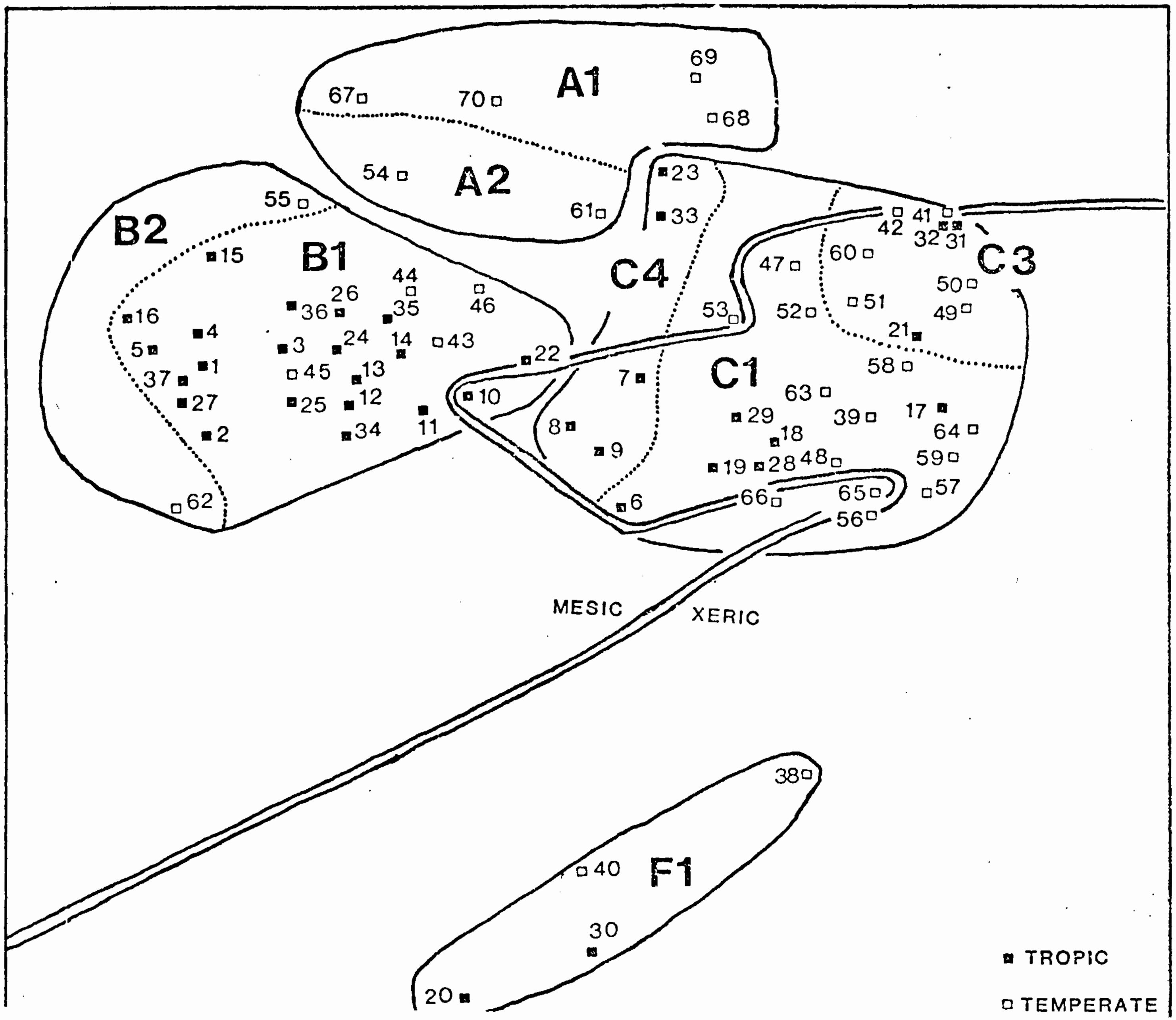
Fig. 16. Multi-dimensional scaling ordination of the southern African specialist frugivore avifauna. The double line represents the 400 mm isohyet. The regions names are listed in Fig. 13. Position of individual quadrats (indicated by numbers) are given in Fig. 13.


A1
A2
B1
B2
C1
C3
C4
F1
MESIC
XERIC
67
70
69
68
54
61
55
23
33
15
16
4
5
1
37
27
2
62
36
26
35
44
46
3
24
14
43
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6
63
29
18
19
28
48
39
17
64
59
57
65
66
56
38
40
30
20
TROPIC
TEMPERATE

ordination bisects provinces F, A & D and also some subprovinces, while the other provinces may be clearly defined as either subtropical or a warm temperate regime.

The African subcontinent is fairly sharply divided into an east-west rainfall gradient (except within the extreme south). In both ordination plots a fairly clear demarcation occurred between mesic (> 400 mm rainfall) and xeric (< 400 mm) areas. The 400 mm isohyet only really bisects province C in the specialist ordination plot (Fig. 16), while only province D and C are bisected on the opportunistic plot (Fig. 15). Thus it seems that provinces and subprovinces arrange themselves in response to a rainfall gradient but not to a tropical-temperate dichotomy.

The number of species characterized (<u>P</u> < 0,05; information statistics tests) per quadrat was meaned over each subprovince. The opportunistic fauna indicates subprovince A2 to possess the most relatively unique fauna and high beta diversities (Fig. 14b). Appendix 3 indicates that for this entire subprovince comprising five quadrats a total of 16 avian species were characterized. Subprovinces A3 and C1 were characterized by 21 and 17 species yet they occupy twice and three times the number of quadrats occupied by A2 respectively. In the specialist map the peak mean number of characterized species per quadrat occurred in subprovince B2 which is a possible transitional area between a temperate A province and a tropical B province (Fig. 14a). In this case the tropical and mesic subprovince (B1) also tends to have a predominance of characterized species (11 out of a total of 21 characterized species are represented by this subprovince).

Species richness

In terms of species richness per quadrat for the specialist and opportunist faunas a basically similar pattern resulted (cf. Figs 17a & 17b). This is in conflict to the prediction that the specialist frugivore should have an emphasised tropical distribution. A pronounced east-west species richness gradient is represented (Figs 17a & 17b), indicating a possibility that environmental conditions (particularly rainfall) may in part, determine species richness patterns.

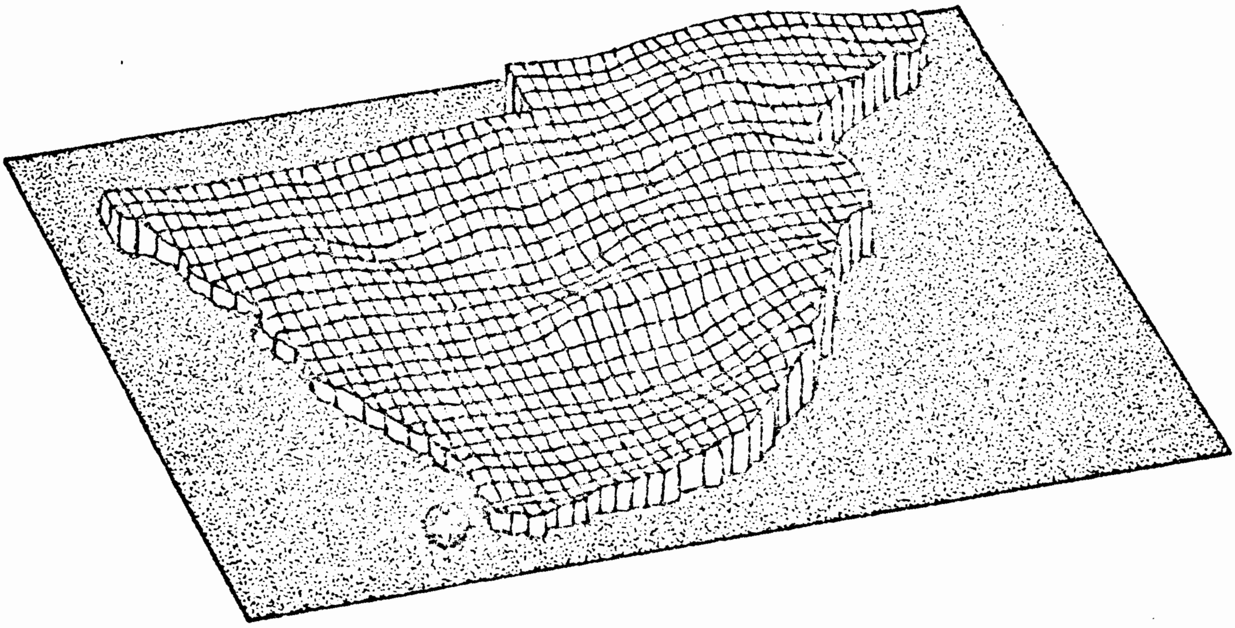
Fruit seasonality

For both the specialist and the opportunist regions a histogram of fruit seasonality for both berry and drupe fruits are represented in Figs 18 & 19 respectively. In Figs 18 & 19 a remarkably similar pattern emerges for all the eastern regions with the peak number of species fruiting for drupe fruits in late summer and the berry fruits in the beginning of autumn. Spring seems to have the fewest species rippening for both drupes and berries. The pattern of fruiting becomes more seasonal in the xeric western half of the continent. The berry fruits become particularly scarce in the late winter and early spring. The length of fruiting season does not vary greatly between the drupaceous and berry fruits, nor is there any pronounced difference in the season length between temperate and tropical areas (Table 22). This is the case in both the opportunist and the the specialist areas. Even between the mesic and the xeric regions there is little change in season lengths (Table 22).

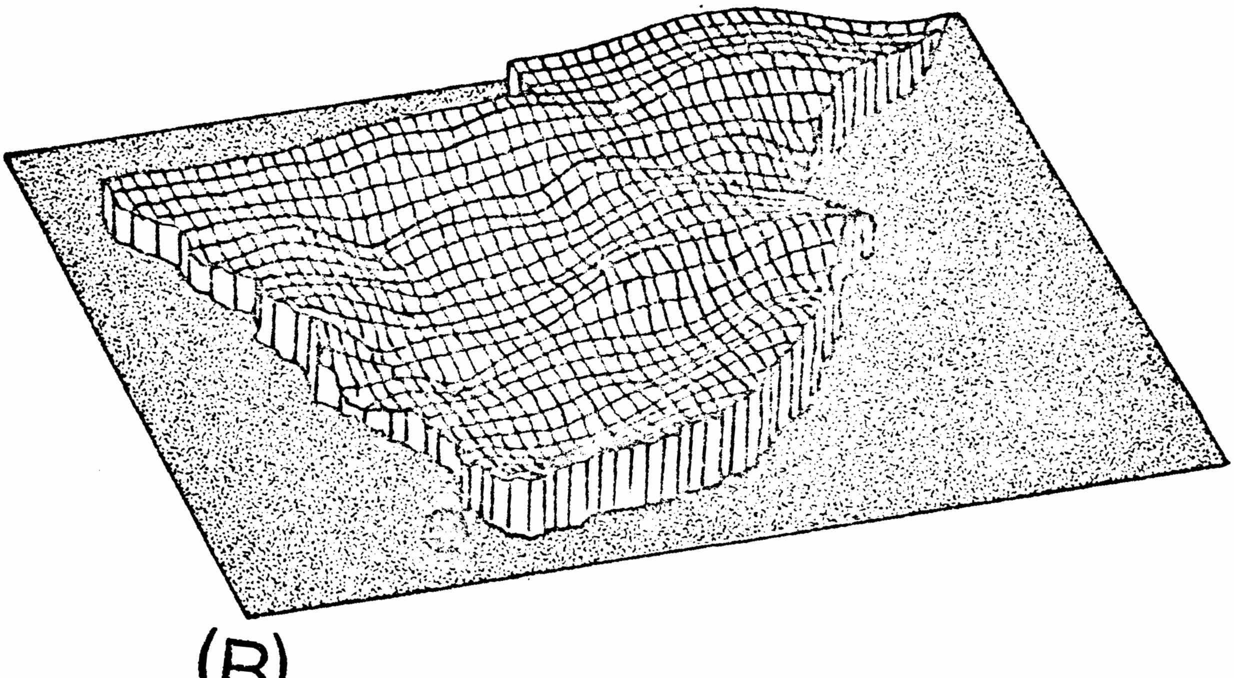
Fruit size

For both the opportunist and the specialist regions a block diagram represents the frequency (as indicated by the area covered

Fig. 17. A Three-dimensional representatioon of the distribution of avian specialist (a) and avian opportunist frugivore species richness (b) in southern Africa. The star indicates the position of Cape Town.



(A)



(B)

Fig. 18. The percentage of tree species presenting drupe and berry fruits according to month and opportunist frugivore region in southern Africa. The upper histogram indicates species bearing berries, while the lower histogram indicates species bearing drupes.

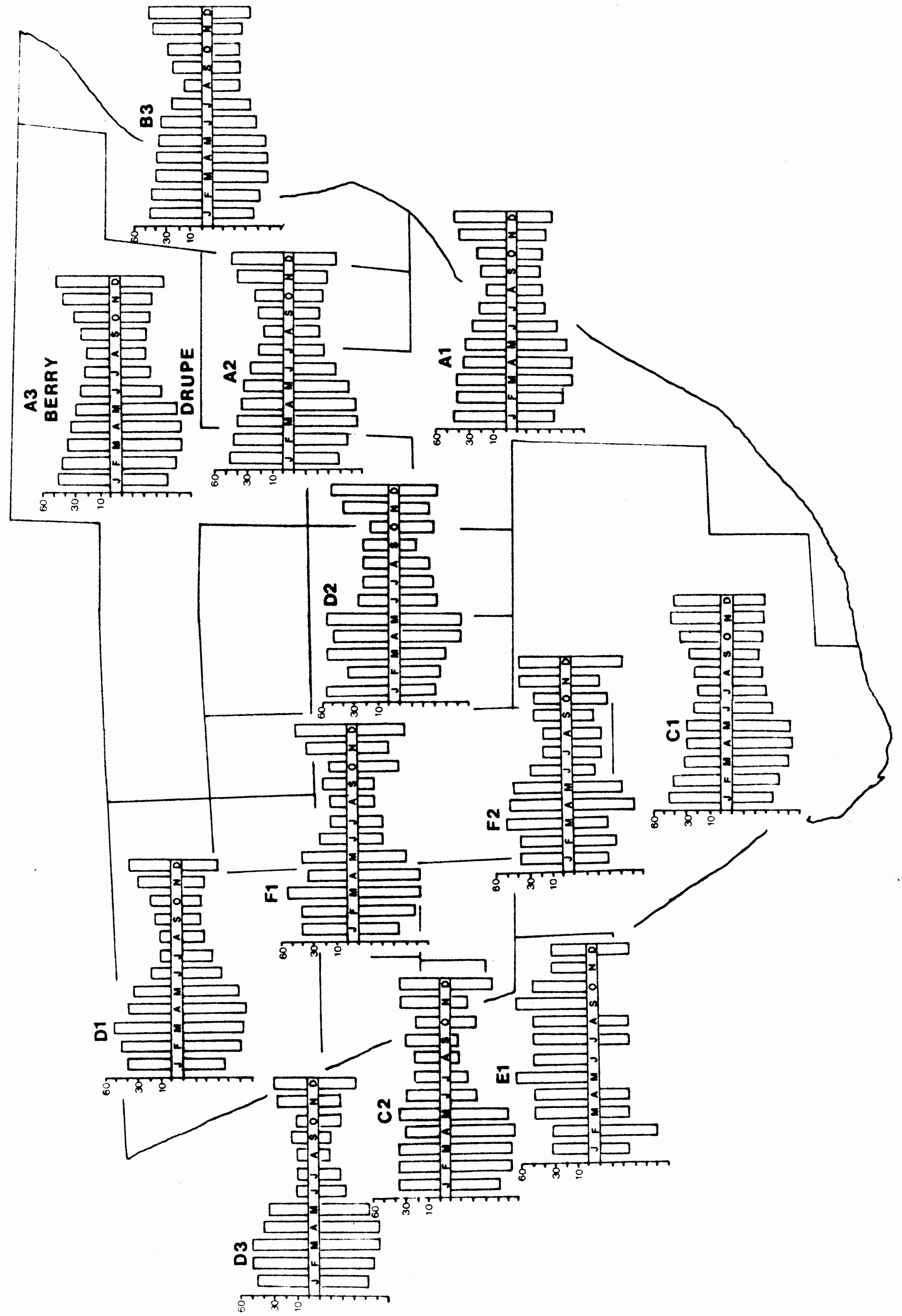

B3
A3
BERRY
DRUPE
A2
A1
D2
C1
F2
F1
D1
E1
C2
D3
J F M A M J J A S O N D
60
30
10

Fig. 19. The percentage of tree species presenting drupe and berry fruits according to month and specialist frugivore region in southern Africa. The upper histogram indicates species bearing berries, while the lower histogram indicates species bearing drupes.

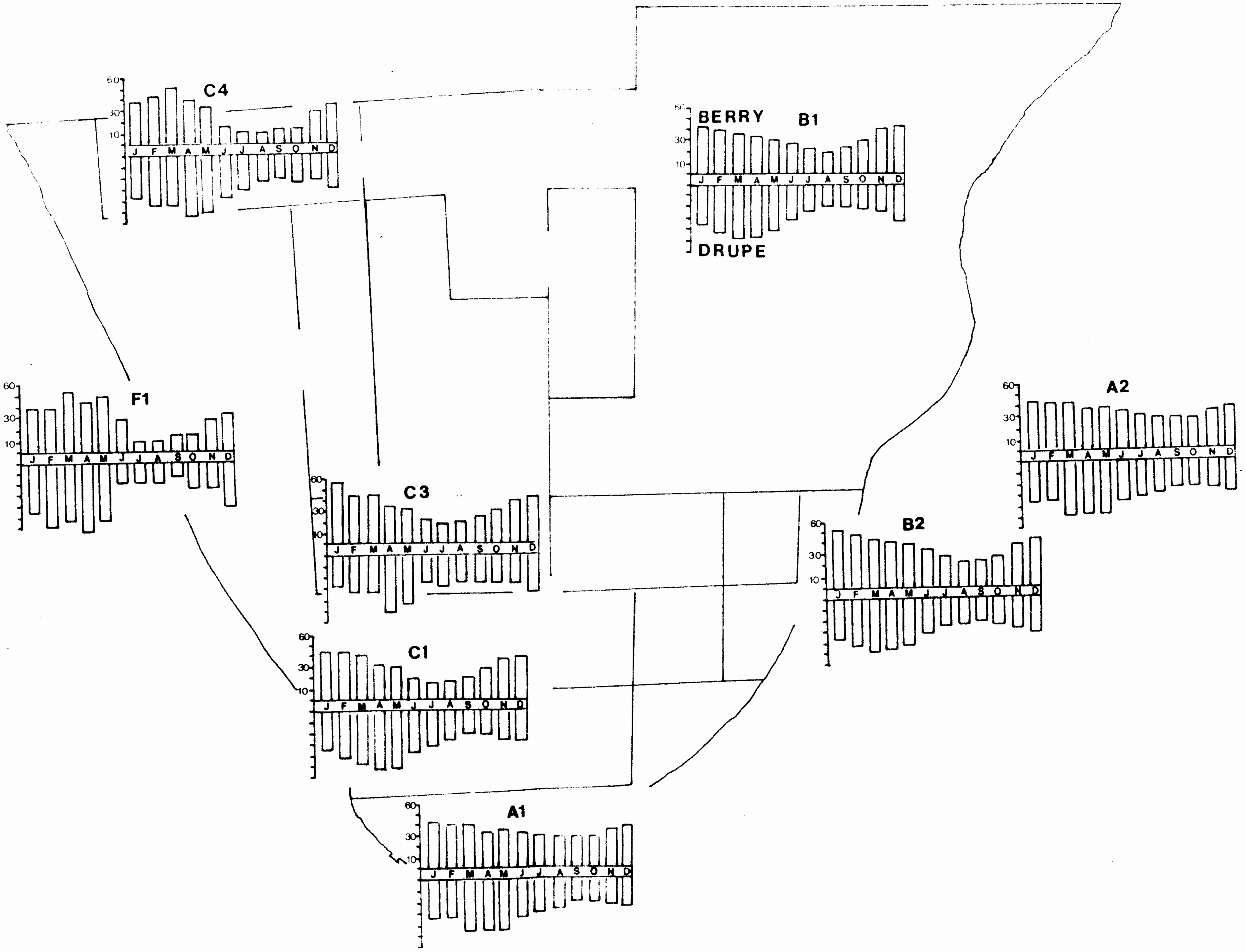

C4
BERRY
B1
DRUPE
F1
C3
A2
B2
C1
A1
60
30
10
J F M A M J J A S O N D

Table 22 Mean duration (in months) of fruit presentation of species bearing drupe and berry fruits for avian opportunist and avian specialist regions.

	Opportunist regions	
	Drupe	Berry
Southern Afromontane (A1)	3,99	4,07
Northern Afromontne (A2)	4,31	4,06
Zimbabwe Northern Bushveld (A3)	4,33	4,11
Mozambique Bushveld (B3)	4,40	4,30
Arid Karoo (C1)	4,21	4,13
Karoo-South Namib (C2)	3,90	3,90
Combretum Savanna/Bushveld (D1)	4;09	3,47
Acacia Bushveld (D2)	4,00	4,54
Northern Namib (D3)	3,72	3,30
West Coast Karoo (E1)	2,00	5,66
S.W.A./Namibia-Kalahari (F1)	3,92	3,95
Peripheral Kalahari (F2)	3,88	3,99
	Specialist regions	
	Drupe	Berry
Southern Afromontane (A1)	4,15	4,27
Northern Afromontane (A2)	4,19	4,85
Bushveld (B1)	4,02	3,86
Southern Coastal Bushveld (B2)	3,98	4,46
Arid Karoo (C1)	3,90	4,11
Karoo-Kalahari (C3)	3,90	4,21
Karoo-Bushveld (C4)	4,20	3,43
S.W.A./Namibia-Kalahari (F1)	4,07	3,75

under the respective rectangles) for each size class of both berry (on the right hand side) and the drupe-bearing species. The solid bar in the centre indicates the proportion of berry-bearing species to drupe-bearing species (Figs 20 & 21). There is a slight tendency for fruit sizes to increase in the subtropical areas in drupe and berry-bearing species. This is indicated by the smaller areas that represent the smallest size class in the temperate areas, while in the subtropics those areas representing the largest fruit size occupy a greater area. This trend is observed in both opportunist and specialist regions (Figs 20 & 21). The trend of larger fruits in the tropics may indicate an increased influence of fruits consumed by mammals. There is also a trend for drupe and berry fruits representing both opportunist and specialist regions to become less predictable in the western arid areas of the subcontinent. There is also a trend for drupe-bearing species to out-number the berry-bearing species, while the largest fruit size class becomes in general better represented, probably indicating a proportional increase in fruits that are eaten (and possibly dispersed) by mammals.

DISCUSSION

Firm evidence for any of the five predictions made in the introduction is not present. In fact the fourth and the fifth predictions that the specialist frugivores should have a tropical but narrow geographical distribution, whereas the opportunist frugivores should have a wider geographical distribution are entirely contradicted on the basis of these analyses. The results obtained may be a consequence of the coarseness of the biogeographical analysis, the reliability and accuracy of published data and the subjective categorization of avian species.

Fig. 20. The percentage of tree species presenting drupe and berry fruits according to size class and opportunist frugivore region in southern Africa. The left hand side represents drupe-bearing species, the right hand side the berry-bearing species, while the shaded part of the central bar indicates the ratio of berry-bearing to drupe-bearing species.

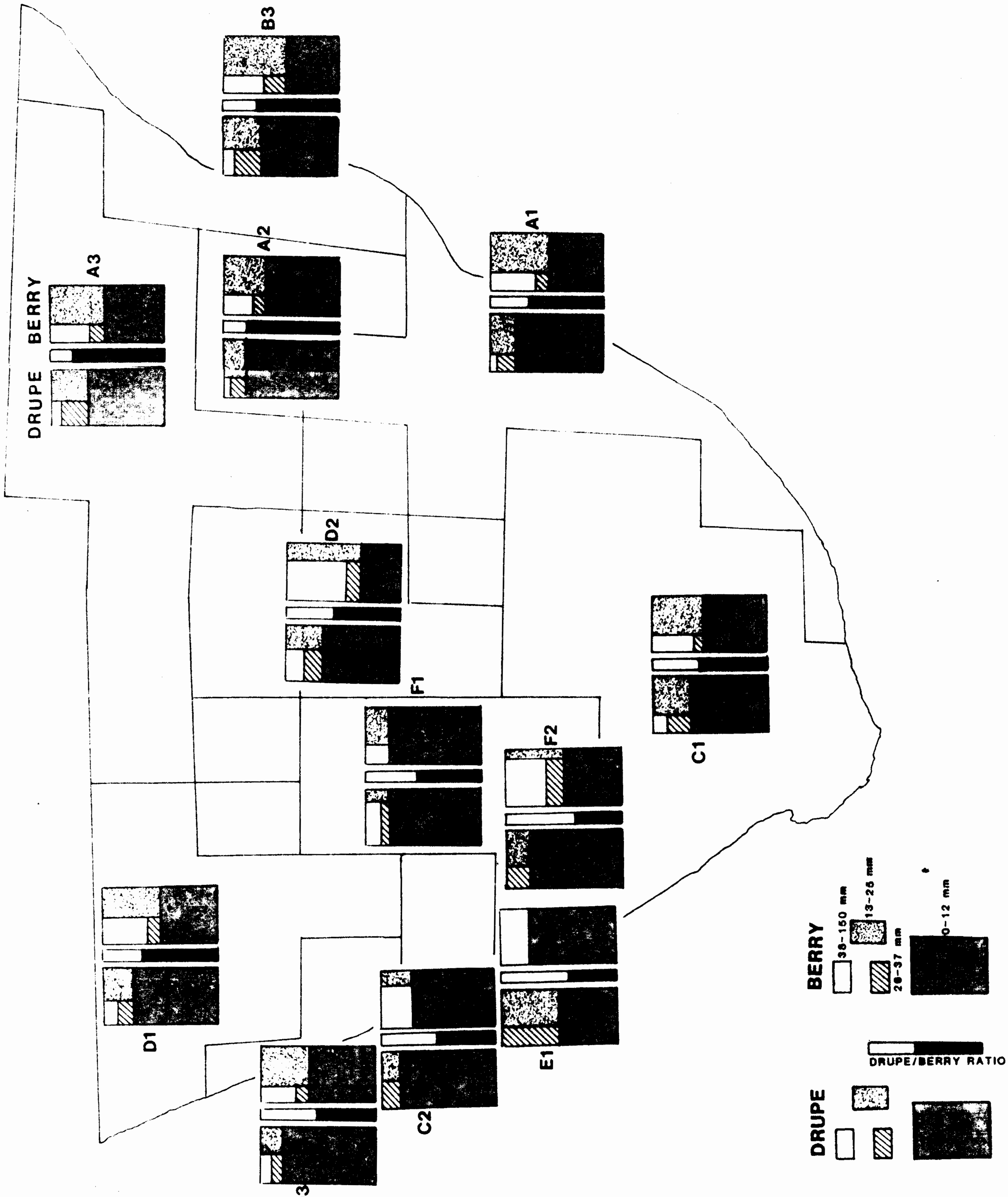
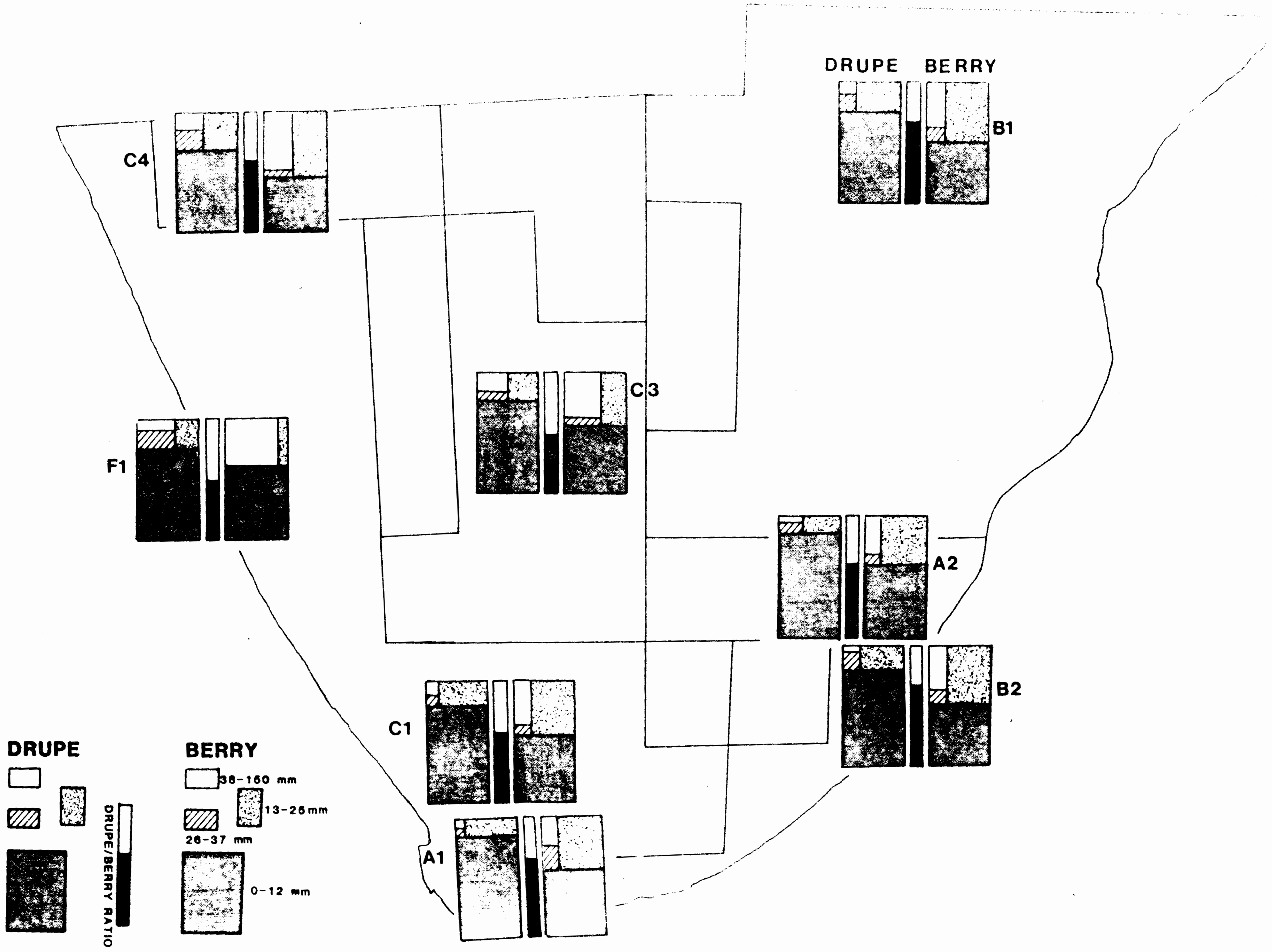

DRUPE
BERRY
A3
A2
B3
A1
D2
C1
F1
F2
D1
E1
C2
D3
BERRY
38-150 mm
13-25 mm
26-37 mm
0-12 mm
DRUPE/BERRY RATIO
DRUPE

Fig. 21. The percentage of tree species presenting drupe and berry fruits according to size class and specialist frugivore region in southern Africa. The left hand side represents drupe-bearing species, the right hand side the berry-bearing species, while the shaded part of the central bar indicates the ratio of berry-bearing to drupe-bearing species.

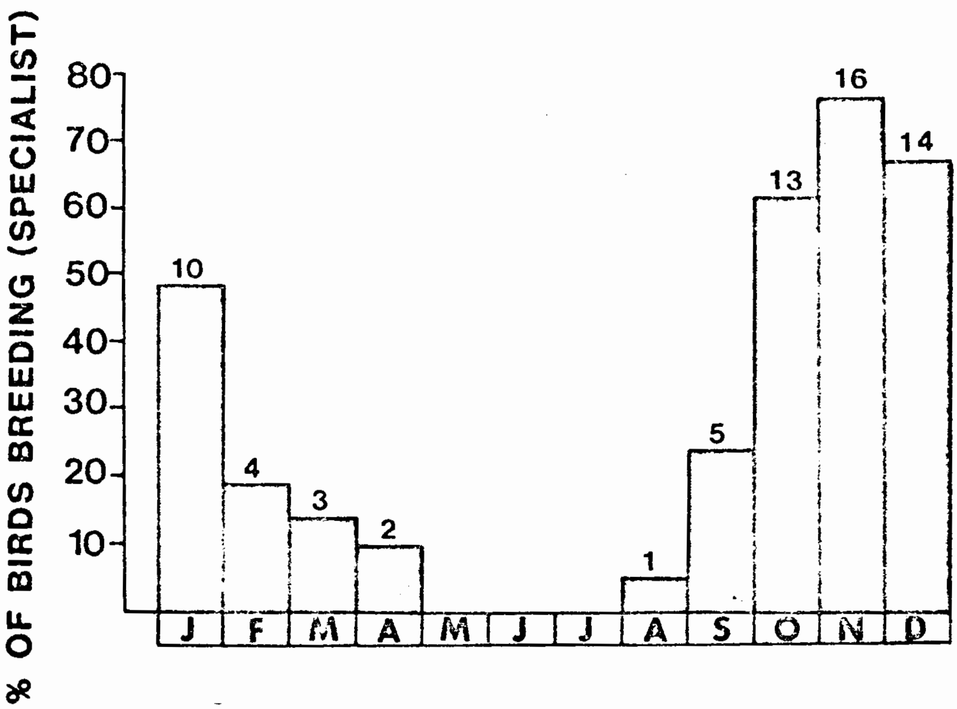

DRUPE
BERRY
B1
C4
C3
F1
A2
B2
C1
A1
DRUPE
BERRY
38-160 mm
13-26mm
26-37 mm
0-12 mm
DRUPE/BERRY RATIO

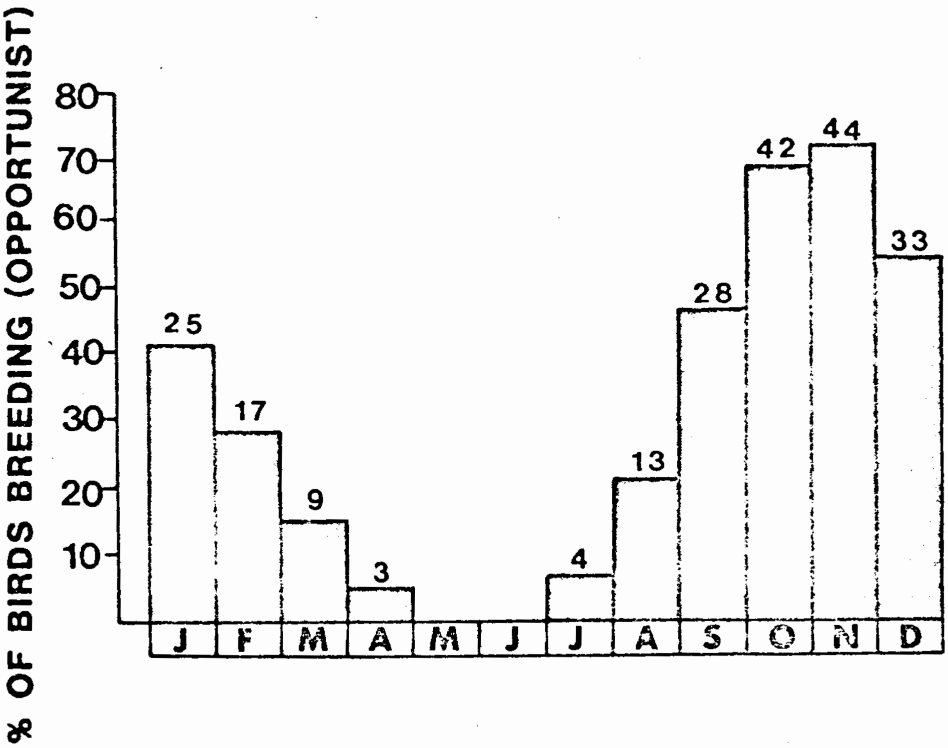
In spite of these limitations there should have been some evidence for a coevolutionary model as proposed by McKey (1975) and Howe & Estabrook (1977).

Although the southern African subcontinent expands a considerable latitudinal range (from subtropical to mediterranean climatic regimes) there was no evidence along this gradient for differences in species richness of berry and drupe-bearing species, possibly the fleshy fruit flora of mediterranean areas are derived from a subtropical flora (see part 2, Milewski, 1982). This may also be reflected in the very similar fruiting phenology that exist for the entire eastern areas of the subcontinent (Figs 18 & 19). There are, however, fairly pronounced differences in terms of fruit sizes and fruiting phenologies between the drupaceous and berry fruits. As a general trend the fruit size of berries is larger, and there is a greater representation of species in the largest fruit size category. This is probably indicative of the berry fruits being more favoured by, or to have "evolved" with potential mammalian dispersal agents. In part 1 it was suggested that relationships may exist between fruit size, fruit colour, fruit type (drupe/berry) and bird or mammal dispersal. These relationships may therefore be indicative of evolutionary linkages between dispersal agents and fruit characteristics. As regards southern Africa, however, there appears to be little evidence of any specific bird/seed-dispersal relationships as proposed by McKey (1975). Frost (1980) has demonstrated that for a South African subtropical coastal forest (at Mtunzini 28°58 S, 31°46 E) that there is a lack of clear differentiation in the sets of frugivores exploiting different quality fruit crops, and that evolutionary linkages between frugivores and fruit characteristics in this community are probably at an intermediate stage.

The throughout-the-year supply of fruit (on a species level) in the eastern half of the subcontinent may be a reflection of selective pressures by birds. Most of the frugivorous birds listed in Appendix 3 are resident and in varying degrees rely on fruit. The consequences of this avian population could be to promote the yearly availability of fruit. A plant species may evolve to supply fruit at periods when other fleshy fruit-bearing plant species are not producing fruit, and may therefore gain an advantage in terms of competing for dispersal agents. In this manner a fairly even supply of fruits may be maintained, although discernable peaks of species fruiting can still occur. Spring and early summer appears to have the fewest species fruiting. This period roughly corresponds with a generalized peak breeding of frugivorous avian species (cf. Figs 18, 19 & 22) based on data in McLachlan (1978). Oatley (1982) has analysed faecal samples of the Starred Robin (Pogonocichla stellata) on a seasonal basis. These results indicate that during the breeding season there is a decline of fruit in the diet, and virtually no fruit is given to nestlings. Whether the decrease in fruit in avian diets during the breeding season is a consequence of selective pressures by birds or birds are merely responding to variations in supply of fruits can only be speculated. The relationships of both fruit size and fruit seasonality seem to be more closely related to a mesic-xeric rather than a tropical-temperate gradient. The fruiting becomes seasonal under xeric conditions, and the fruit sizes become more compatible with mammalian dispersal. In consequence the bird/seed-dispersal relationships in southern Africa are likely to be influenced more by enviromental conditions than evolutionary processes. In conclusion the recentness of much

Fig. 22 . A generalized breeding season for (a) specialist avian frugivores (N = 21) and (b) for opportunist avian frugivores that occur in southern Africa (N = 61). Data was taken from McLachlan (1978). The numbers above each bar indicates the absolute frequency.


% OF BIRDS BREEDING (SPECIALIST)
80
70
60
50
40
30
20
10
10
4
3
2
1
5
13
16
14
J
F
M
A
M
J
J
A
S
O
N
D


% OF BIRDS BREEDING (OPPORTUNIST)
80
70
60
50
40
30
20
10
25
17
9
3
4
13
28
42
44
33
J
F
M
A
M
J
J
A
S
O
N
D

of the avian fauna in southern Africa may have prevented close relationships with plant species being established (Snow 1981).

The pattern of fruit seasonality is the most visible consequence of any possible evolutionary relationship between birds and seed-dispersal. This situation may be compared to Europe and America where there appears to be well defined relationships between fruiting seasons and the influx of migrating frugivores (Herrera, 1982, Stapanian, 1982, and Stiles, 1979) whereas other evolutionary relationships have not been established.

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CONCLUSION

This project attempted to synthesize biogeographical and evolutionary aspects of reproductive angiosperm biology in southern Africa in terms of a quantified holistic methodology. The use of Coates Palgrave's (1977) maps are not ideal as these do not represent an atlas of tree species but are an aid to identification. They remain, however, the only available source on tree distributions. The results obtained represent quantified hypotheses, and intensive and individual studies are now required to test the validity of these hypotheses. These hypotheses are related to _a priori_ predictions that have recently been published on biogeographical patterns of seed-dispersal and plant/animal relationships. There appear to be many discrepancies between the results obtained in this study and _a priori_ literature prediction. This is perhaps due to the fact that most research has centred on the Neotropics and temperate Europe and North America. There are, however, a number of more specific conclusions that can be drawn from this analysis.

A minimum of 23% of the southern African tree flora are known to be dispersed by birds, while up to 52% of this flora is likely to be dispersed by either birds or mammals. Fleshy fruits and vertebrates are the most common technique for the dispersal of tree species propagules. The fruits of bird dispersed species are usually small and brightly coloured (red or black) whereas fruits of mammal dispersed species tend to be large and dull (yellow or green). For species possessing berry, drupe, capsule or nut fruits the biogeographical patterns of species similarity accord with both latitudinal (tropical-temperate) and longitudinal (mesic-xeric) gradients. Drupe and pod-bearing species predominate in the xeric areas, berry-bearing species in the mesic areas and nut-bearing species in the temperate areas. In general, species richness patterns for species bearing these fruits reflect a mesic-xeric rather than a tropical-temperate gradient. Pod, berry and drupe-bearing species richness patterns appear to be partly environmentally dependent, while fruit size and fruit colour, although independent of each other, relate to fruit type and to a suite of environmental parameters. The aril-bearing tree species appear to be the most environmentally tolerant flora and are capable of occupying expansive geographical ranges. Such features are not consistent with their being a primitive group and although they may have had a longer ancestry than other fleshy fruit bearing trees they appear as a highly evolved and successful group in the African tree flora. The relationship of both the specialist and the opportunist frugivorous avifauna with the tree flora does not appear to be reflected in latitudinal (tropical-temperate) changes, but such relationships do appear to change in response to environmental conditions (increasing aridity).

The southern African tree flora and the avifauna is thought to have experienced widespread extinction during past glacial periods of enhanced aridity. Such conditions may have prevented the development of exclusive reciprocal relationships between tree species and frugivores. A fluctuating environment would tend to favour a plasticity in plant/animal relationships. The indigenous southern African tree flora, however, is now complemented by 722 introduced tree species (Anon. 1981). As a result of this avian plasticity those alien species possessing arillate or fleshy fruits (e.g. _Acacia cyclops_, _Lantana camara_, _Myoporum insulare_, _Pittosporum undulatum_, _Rubus_ spp., _Solanum mauritianum_, _Psidium_ *guajava*, *Hedychium flavum* and *Melia azedarach*) are able to exploit the indigenous avifauna for seed dispersal. The increase in number and abundance of alien tree species dispersed by the indigenous avifauna is becoming a key management problem.

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Maximum likelihood statistic

For a goodness of fit measure in our multi-dimensional contingency table models, we could have used Pearson's statistic $\chi^2 = \Sigma(0-E)^2/(E)$. However, Pearson's approximation of the maximum likelihood estimate $G^2 = (2\Sigma \log_e 0/E)$ is not valid under certain conditions (Williams 1976b). Therefore, the G^2, which is no longer computationally inconvenient to calculate, was used. Brown (1973) has established that G^2 has the advantage of being additive under partitioning, i.e. if M1 and M2 are two models such that the marginals fitted by M1 are a subset of those fitted by M2 then

$$G^2\ (M1) = G^2\ (M1/M2) + G^2\ (M2).$$

Therefore, this goodness of fit measure is universally used in preference to the normal Pearson's statistic.

Appendix 2. The southern African arillate-bearing tree flora in relation to five major regions: (A) Bushveld, (B) Northern Namib, (C) Mozambique Coastal, (D) Arid Karoo, and (E) Subtropical Coastal. XX and X indicates the species to be characteristic (information statistic test) at *P* < 0,01 and *P* < 0,05, respectively, for each region.

	Arillate regions				
Species	A	B	C	D	E
Albizia adianthifolia	XX				
Albizia amara					XX
Bersama abyssinica				XX	
Bersama lucens					XX
Bersama stayneri	XX				
Bersama transvaalensis	XX				
Bersama tysoniana					XX
Casearia battiscombei			XX		
Casearia gladiiformis	XX				
Cassipourea mossambicensis	XX				
Catha transvaalensis					XX
Commiphora africana	XX	XX			
Commiphora anacardiifolia			X		X
Commiphora angolensis					XX
Commiphora caerulea	XX				
Commiphora crenato-serrata	XX				
Commiphora dinteri	XX				XX
Commiphora edulis	XX				
Commiphora glaucescens					XX
Commiphora harveyi	XX				

Appendix 2 cont.

Species	Arillate regions				
	A	B	C	D	E
Commiphora karibensis	XX				
Commiphora marlothii	XX				
Commiphora merkeri	XX				
Commiphora mollis					
Commiphora namaensis			XX		
Commiphora neglecta		XX			
Commiphora oblanceolata	XX				
Commiphora pyracanthoides					
Commiphora schimperi	XX				
Commiphora schlechteri	XX				XX
Commiphora serrata	XX				
Commiphora tenuipetiolata			XX		XX
Commiphora ugogensis				XX	
Commiphora virgata	XX				
Commiphora wildii		XX			
Commiphora woodii	XX				
Commiphora zanzibarica	XX				
Exoecaria bussei				XX	XX
Guibourtia coleosperma	XX				
Macaranga capensis					XX
Maytenus acuminata				XX	X
Maytenus bachmannii				XX	
Maytenus chasei	XX				
Maytenus heterophylla				XX	XX
Maytenus linearis	XX		XX		XX

Appendix 2 cont.

	Arillate regions				
Species	A	B	C	D	E
Maytenus lucida			XX		XX
Maytenus mossambicensis					XX
Maytenus oleoides				XX	XX
Maytenus penduncularis					XX
Maytenus polyacantha					XX
Maytenus procumbens					
Maytenus putterlickioides			X		XX
Maytenus senegalensis				XX	
Maytenus undata					XX
Pseudobersama mossambicensis	XX				
Putterlickia pyracantha					XX
Putterlickia sp no 1	XX				
Putterlickia verrucosa					
Schotia afra	XX				
Schotia brachypetala					XX
Schotia capitata				XX	
Sterculia africana					XX
Strelitzia alba				XX	
Strelitzia caudata	XX				
Strelitzia nicolai					XX
Trichilia capitata					
Trichilia dregeana			XX		XX
Trichilia emetica				XX	
Zanha africana				XX	
Zanha golungensis					

Appendix 3

The southern African frugivorous avifauna in relation to opportunist and specialist regions. A1 = Southern Afromontane, A2 = Northern Afromontane, A3 = Zimbabwe Northern Bushveld, B1 = Bushveld, B2 = Southern Coastal Bushveld, B3 = Mozambique Bushveld, C1 = Arid Karoo, C2 = Karoo-South Namib, C3 = Karoo-Kalahari, C4 = Karoo-Bushveld, D1 = Combretum Savanna/Bushveld, D2 = Acacia Bushveld, D3 = Northern Namib, E = West Coast Karoo, F1 = S.W.A. /Namibian Kalahari, F2 = Peripherial Kalahari.

	Opportunist avifauna regions											
	A1	A2	A3	B1	C1	C2	D2	D1	D3	E	F1	F2
Gypohierax angolensis	XX	XX	XX									
Guttera pucherani			XX									
Streptopelia semitorquata	XX											
Colius striatus								XX				
Colius colius							XX		X			
Colius indicus		XX				X						
Tockus nasutus					XX							
Tockus erythrorhynchus		XX			XX							
Tockus flavirostris	X		XX					XX				
Tockus alboterminatus			XX									
Tockus bradfieldi	XX		X									
Tockus monteiri								XX				X
Oriolus auratus					XX							
Oriolus larvatus		X			XX							
Oriolus chlorocephalus			XX					XX				
Corvus capensis	XX	X			XX							

	A1	A2	A3	B1	C1	C2	D2	D1	D3	E	F1	F2
Corvus albus					XX							
Corvus albicollis												
Lioptilus nigricapillus			XX									
Pycnonotus capensis			XX									
Pycnonotus nigricans								XX	XX			
Pycnonotus barbatus				XX			XX					
Phyllastrephus flavostriatus		XX				XX						
Andropadus importunis	XX		XX									
Andropadus milanjensis						XX				XX		
Andropadus insularis					XX		X					
Chlorocichla flaviventris					XX							
Turdus libonyana		XX	XX									
Turdus olivaceus	XX		XX				X					
Monticola rupestris								XX				
Monticola explorator							XX				X	
Thamnolaea cinnamomeiventris		XX		XX								
Cossypha heuglini	XX											
Cossypha dichroa		XX			XX					XX		
Cossypha natalensis					XX							
Cossypha caffra			XX									
Cossypha humeralis			XX									
Cichladusa arquata		XX								XX	X	
Erythropygia coryphaeus								XX	XX			
Erythropygia leucophrys							XX					
Pogonocichla stellata		XX		XX								
Namibornis herero					XX	X						
Parisoma subcaeruleum		X	XX	XX								
Creatophors cinerea	X	XX	X									
Cinnyricinclus leucogaster	X		XX									
Spreo bicolor			XX									

Lamprotornis nitens		X						XX	X			X
Lamprotornis chalybaeus					XX		XX					
Lamprotornis chloropterus		XX	XX			XX						
Lamprotornis corruscus					XX							
Lamprotornis acuticaudus					XX							
Lamprotornis mevesii	XX		XX									
Lamprotornis australis	X		XX						X			
Zosterops pallidus								XX				
Zosterops senegalensis							XX					
Bubalornis niger		XX		XX								
Serinus scotops					XX							
Serinus sulphuratus					XX							
Serinus albogularis								XX				
Serinus gularis	X		XX									
Serinus mennelli					X			XX				
	13	16	21	5	17	5	8	11	5	3	2	2

Specialist avifaunal regions

	A1	A2	B2	B1	C1	C3	C4	F1
Columba arquatrix	XX		XX	XX				
Columba delegorguei				XX				
Treron calva				XX				
Tauraco corythaix					XX		XX	
Tauraco porphyreolophus			X					
Corythaixoides concolor		X		XX				
Bycanistes bucinator				X	XX		XX	
Bycanistes brevis					XX			
Lybius torquatus				XX				
Lybius leucomelas				XX				
Lybius chaplini			XX				XX	

Stactolaema leucotis								
Stactolaema whytii					XX		XX	
Pogoniulus olivaceus			XX				XX	
Pogoniulus pusillus				XX				
Pogoniulus chrysoconus	XX	XX			XX			
Pogoniulus bilineatus				XX				
Pogoniulus simplex					XX		XX	
Trachyphonus vaillantii	XX		XX					
Onychognathus morio				X				
Onychognathus nabouroup				XX				
	3	2	5	11	6	0	6	0

Appendix 4

DISTRIBUTION AND SPECIES RICHNESS OF TREES IN SOUTHERN AFRICA

R.S. Knight, T.M. Crowe and W.R. Siegfried

(For reference purposes only, not to be assessed as part of the thesis)

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DISTRIBUTION AND SPECIES RICHNESS OF TREES IN SOUTHERN AFRICA*

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ABSTRACT

A phytochorology for southern Africa is derived, based exclusively on species of trees. Cluster analysis, multi-dimensional scaling and information statistic tests are applied to isolate and characterize assemblages of tree species. Six major tree provinces, three of which contain a number of subprovinces, are recognized in a two-tier classification scheme. This phytochorology is compared with classification schemes based on subjective decisions and qualitative information. Correlation and regression analyses involving a suite of environmental variables are used in examining hypotheses concerning an increase in species richness with a decrease in geographical latitude, and a decrease in species richness with an increase in aridity.

UITTREKSEL

DISTRIBUSIE EN SPESIERYKHEID VAN BOME IN SUIDELIKE-AFRIKA*

In hierdie artikel word 'n fitochorografie vir Suider-Afrika voorgestel wat uitsluitlik gebaseer is op boomspesies. Groepe boomspesies word onderskei en gekarakteriseer deur middel van groepanalises, multidimensionele gradering en die toepassing van statistiese inligtingstoetse. Ses hoofboomgebiede waarvan drie in aantal subgebiede insluit, word onderskei. Die voorgestelde fitochorografie word vergelyk met klassifikasiestelsels wat op subjektiewe beslissings en kwalitatiewe informasie gebaseer is. Korrelasie- en regressieanalises wat 'n stel omgewingsveranderlikes behels, word gebruik om hipoteses oor 'n toename van spesierykheid met afnemende geografiese breedte en 'n afname van spesierykheid met toenemende dorheid te ondersoek.

INTRODUCTION

Southern African phytochorological studies (reviewed by Werger, 1978) tend to rely on unspecified data bases, and the criteria used to delimit phytochoria have frequently been undefined. Here we report a phytochorology for southern Africa based, for the first time, exclusively on trees, and modern analytical methods. In discussing the derived patterns of geographical

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* This paper constitutes part of the commemoration of the 21st anniversary of the establishment of the Percy FitzPatrick Institute of African Ornithology.

* Hierdie artikel maak deel uit van die 21ste herdenking van die stigting van die Percy FitzPatrick Instituut vir Ornitologie van Afrika.

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distribution and species richness of the southern African tree flora, we examine hypotheses which have been advanced in explanations for the distribution of trees in other regions (Monk, 1967), or other major groups of plants or animals (Fischer, 1960; Williams, 1964; Pianka, 1966; Recher, 1971; Werger, 1978; McCoy and Connor, 1980). More particularly, we examine the following predictions: there should be an increase in species richness with a decrease in geographical latitude; and, there should be a decrease in species richness with an increase in aridity.

MATERIAL AND METHODS

The main data base was assembled from 1 362 distributional maps for indigenous tree species in Coates Palgrave (1977). These maps summarize records lodged at herbaria in southern Africa and represent the localities of occurrence enclosed within a continuous boundary, and cover all political states south of S 15°, except for Mozambique for which only the area south of the Zambezi River was included. Further, these maps do not represent an atlas of tree species but an aid to identification; however, they remain the only available source on tree distributions. With the concomitant increase in data base accuracy and resolution together with the refinement of analytical techniques (to increase data handling capabilities) the phytochorology for southern African trees based on quantified approaches will improve. A grid of 70 quadrats (Fig. 1) was used to transform each map into a numerical form; each quadrat being scored for each species according to a 1–10 scale, with each of the 10 numerals accounting for 10 % of the area of each quadrat and thus results in a 95 340 cell matrix.

Cluster analysis (Field and McFarlane, 1968; Anderberg, 1973) and multidimensional scaling (Kruskal, 1964) were used to identify groups of quadrats with similar species compositions. These two methods allow relatively objective and repeatable determination of potential patterns of sample grouping, based on all measured attributes (i.e. species) considered simultaneously and equally (Sneath and Sokal, 1973; Clifford and Stephenson, 1975). Information statistic tests (Field, 1969) were used to determine the species which characterize ($P < 0,01$) the groups of quadrats. The distribution of the most characteristic species was used in conjuction with the cluster analysis and ordination to produce a final pattern of tree assemblages. The species richness for each quadrat was subjected to a contouring programme (S. G. P. Diederiks, 1979) which fitted a surface, by a least squares polynomial analysis, to the data for visual representation.

Correlation and stepwise multiple linear regression analyses (Sokal and Rohlf, 1969; Allen, 1973) were used to determine possible relationships between species richness (the dependent variable) and ten measures of the en-

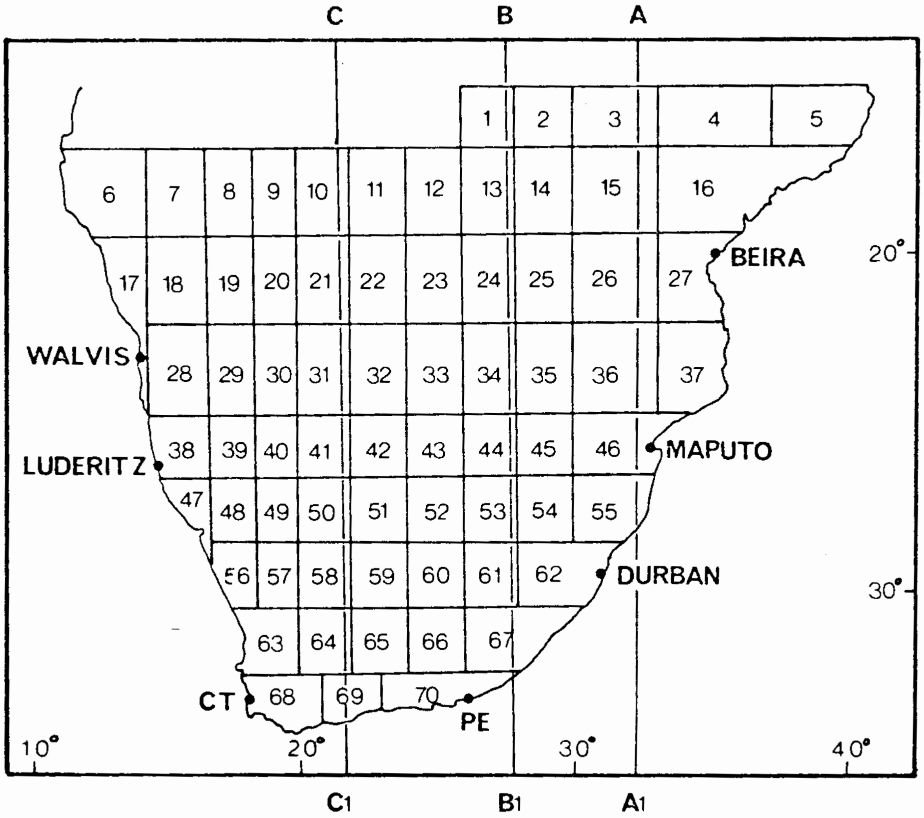


FIG. 1
The grid of quadrats (numbered 1–70) used in an analysis of the distribution of tree species in southern Africa. The lines A–A1, B–B1 and C–C1 represent transects (see Fig. 6).

vironment (the independent variables): mean annual solar radiation (ANNRAD); mean annual temperature (XTEMP); mean annual temperature range (TRANGE); January maximum temperature (TMAX); July minimum temperature (TMIN); mean annual rainfall (XRF); range in annual rainfall (RRANGE); altitudinal range (ARANGE); water surplus (WPLUS); and, actual evaporation (AE). These environmental data were taken from Talbot and Talbot (1960); Jackson (1961); Thornthwaite (1962); Clark (1967); and Schulze and McGee (1978).

RESULTS

A line drawn at the 20 % similarity level across the dendrogram showing clusters of species assemblages (Fig. 2) separates six groups or provinces

(A–F), which were also distinct in multi-dimensional scaling (Fig. 3). Within three of these provinces, smaller clusters were identified between the 35 and 45 % similarity levels, and were designated as subprovinces (Figs. 2 & 3). The geographical boundaries of these areas are shown in Figure 4a. Figure 5 shows that species richness is relatively high in the eastern portion of the subcontinent, but there are few, if any, signs of an increase in species richness with a decrease in latitude (Fig. 6). Species richness is correlated positively and most strongly with mean annual rainfall (Fig. 7, Table 1). The second most strongly, though negatively, correlated environmental variable is mean annual solar radiation (Fig. 8, Table 1). The environmental variable with the second highest coefficient of determination is altitudinal range (Fig. 9, Table 1). Table 2 summarizes the results of the stepwise multiple regression analysis.

DISCUSSION

Phytochorology

Werger's (1978) phytochorology for southern Africa includes a Karoo-Namib region north of a Capensis subkingdom. He recognizes five domains within the Karoo-Namib region: Namib, Namaqualand, South Kalahari, Western Cape, and Karoo. In our subdivision of southern Africa, the Karoo province stretches much farther eastwards, but not as far northwards. Moreover, our Kalahari province is more distinctive, our belt along the Indian Ocean extends much farther inland, and Werger's (Fig. 4b) Namib region is split into northern and southern parts. There is also a minor difference, in that our Afro-montane Forest and Alpine Veld is more continuous than Werger's (Fig. 4b) and more closely approximates White's (1978) distribution of the division (Fig. 4c). White's Afro-montane archipelago includes two major assemblages for southern Africa, the Chimanimani in the north (comparable to our Zambezian Montane Forest) and the Drakensberg in the south (comparable to our Afro-montane Forest and Alpine Veld). However, unlike White's scheme, our eastern Karoo stretches to the western boundary of the Afro-montane Forest and Alpine Veld.

Other differences between White's scheme and ours are that he seems to have drawn little distinction between the Namib and the Karoo and in accordance with most other phytogeographers he does not recognize a separate Kalahari area.

Our phytochorological arrangement deviates from all other schemes in that we do not identify a strikingly distinct Capensis area; instead, we include a Capensis element at a second-order subprovince level. The main reason for this discrepancy rests in the selection of trees only for this study,

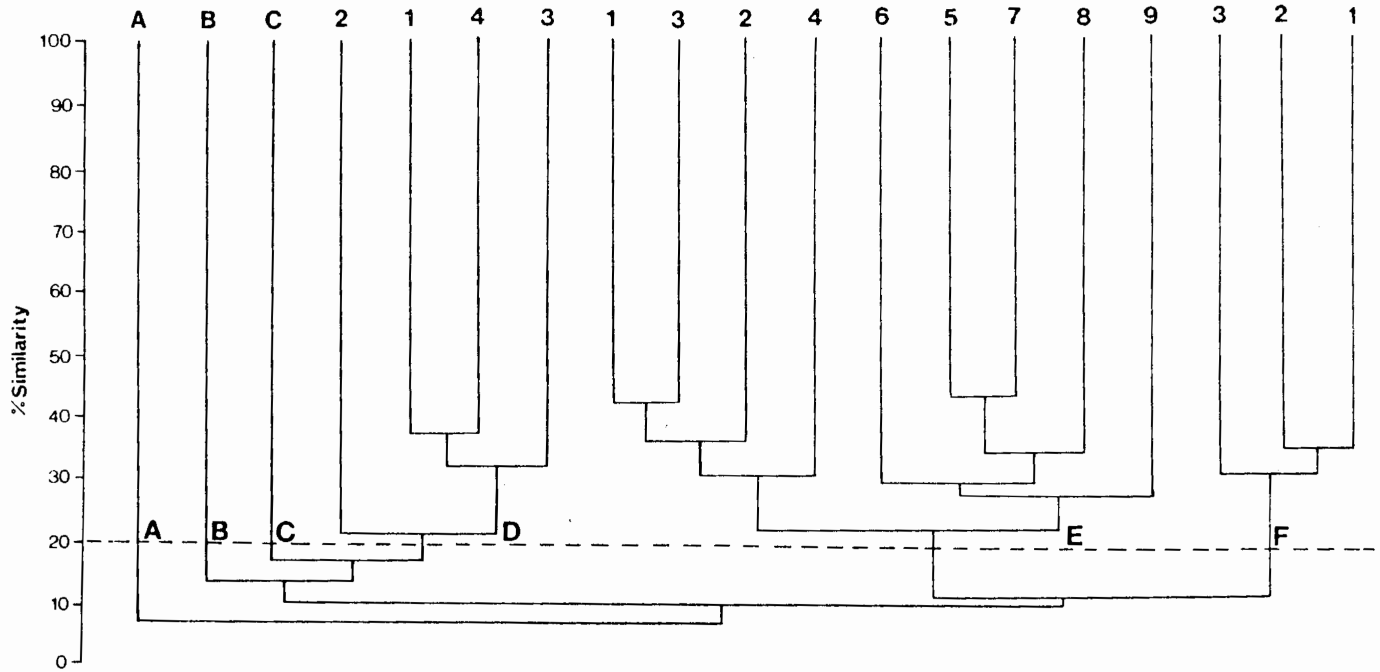


FIG. 2
The result of cluster analysis of 70 quadrats according to their tree species in southern Africa.

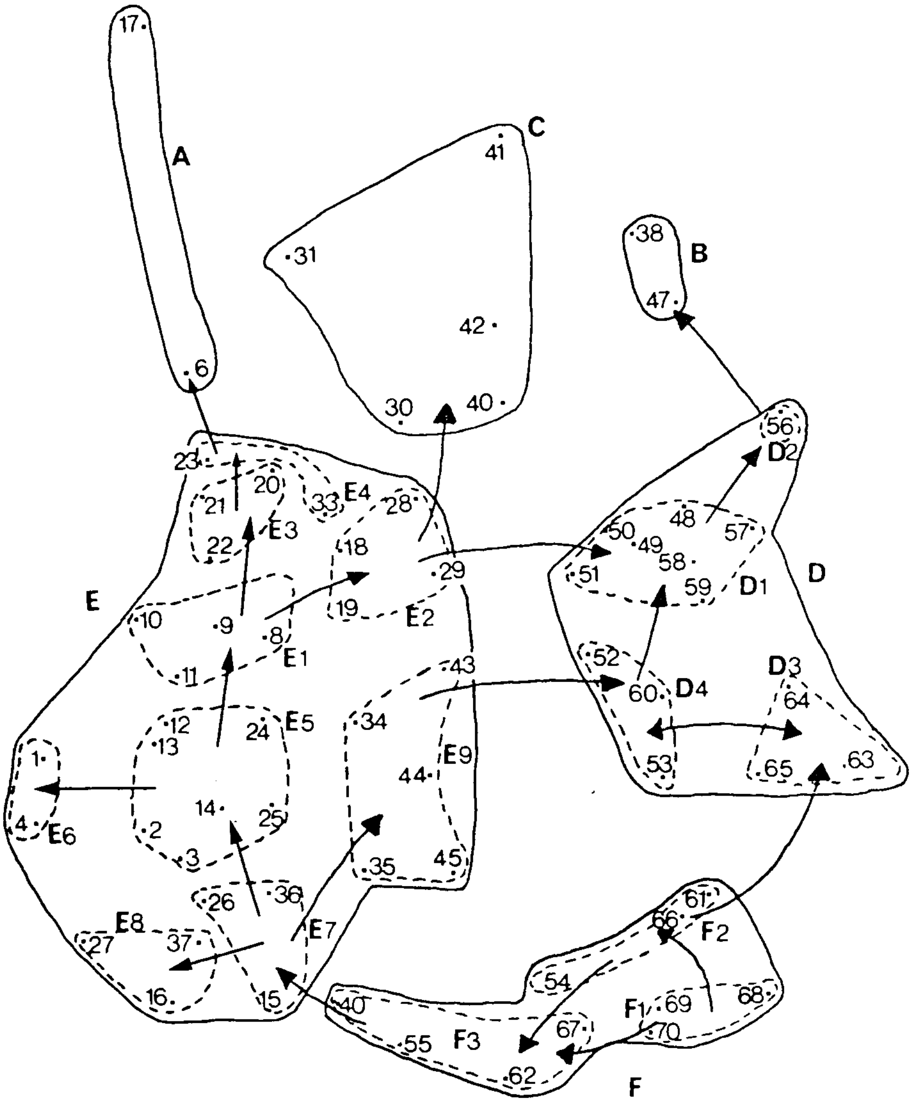


FIG. 3
The result of multi-dimensional scaling of 70 quadrats according to their tree species in southern Africa. The arrows indicate possible routes of species radiation.

TABLE 1

Correlation coefficient matrix of tree species richness and 10 environmental variables in southern Africa. SR = species richness, ANNRAD = annual solar radiation, XTEMP = mean annual temperature, TRANGE = annual temperature range, TMAX = maximum January temperature, TMIN = minimum July temperature, XRF = mean annual rainfall, RRANGE = annual range of rainfall, ARANGE = altitude range, WPLUS = water surplus, and AE = actual evaporation.

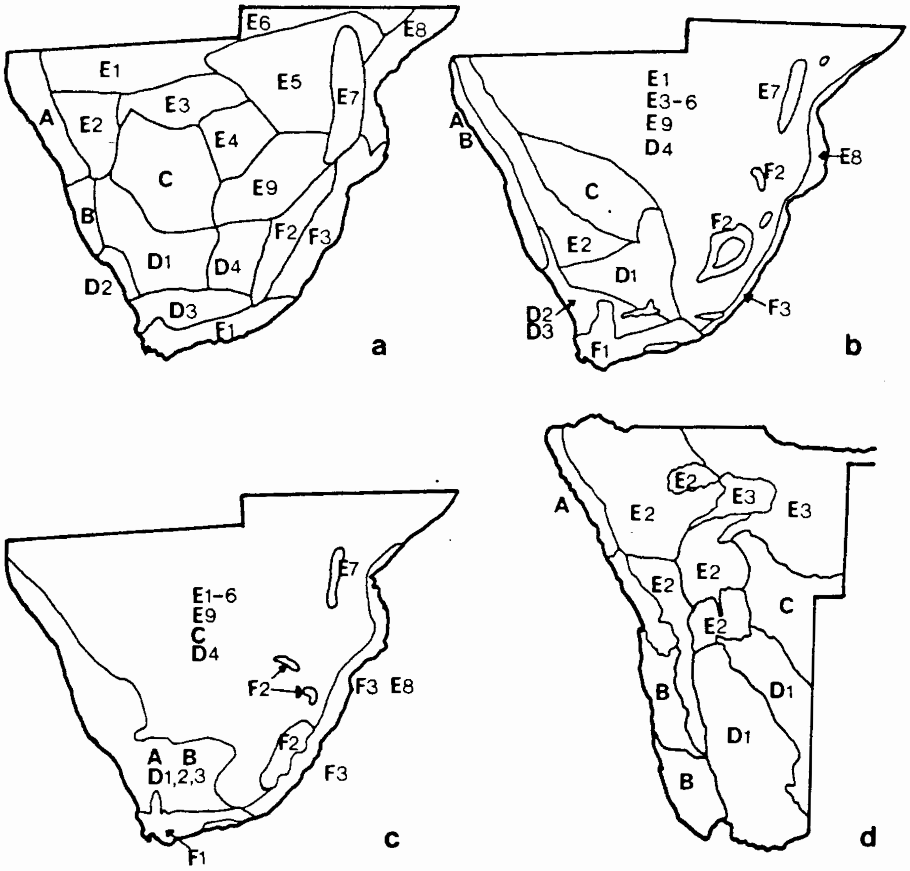
NAME	SR	ANNRAD	XTEMP	TRANGE	TMAX	TMIN	XRF	RRANGE	ARANGE	WPLUS	AE
SR											
ANNRAD	–0,622 *										
XTEMP	0,211	0,121									
TRANGE	–0,525	0,555	–0,106								
TMAX	–0,143	0,342	0,484	0,551							
TMIN	0,273	–0,262	0,471	–0,756	–0,174						
XRF	0,641	–0,605	0,223	–0,400	–0,079	0,195					
RRANGE	0,527	–0,564	0,043	–0,499	–0,087	0,291	0,626				
ARANGE	0,492	–0,575	–0,456	–0,451	–0,560	0,038	0,301	0,403			
WPLUS	0,469	–0,459	0,247	–0,481	0,078	0,380	0,565	0,460	0,255		
AE	0,576	–0,531	0,177	–0,306	–0,136	0,107	0,942	0,552	0,250	0,290	

* Critical values of r for significance levels are: $r = 0{,}235$; $p = 0{,}05$; $r = 0{,}306$; $p = 0{,}01$.

TABLE 2

Results of stepwise regression analysis between quadrat tree species numbers and the environmental variables listed in Table 1 for southern Africa. XRF = mean annual rainfall, ARANGE = altitude range, XTEMP = mean annual temperature, and ANNRAD = mean annual radiation.

Variable	Coefficient of determination (R^2)	Regression Coefficient (Z)
XRF	0,41	0,41
ARANGE	0,50	0,07
XTEMP	0,59	22,96
ANNRAD	0,62	-2,77



thereby excluding the majority of the Capensis flora. However, there is also increasing evidence in favour of elements of the Capensis flora having affinities with the Alpine Veld of Lesotho (Killick, 1978).

The relatively large area of the Karoo province in our scheme may also be due to the selection of trees only. Trees are relatively sensitive to arid conditions, and all relatively dry areas may have been included in the Karoo simply because their trees are of a Karoo type, whereas the annual vegetation belongs to a different biotype. Although our Karoo, Kalahari and two Namib areas in South West Africa/Namibia do not conform with other generalized schemes (Fig. 4b), they do agree fairly closely with the vegetation types in Giess's (1970) map of the territory (Fig. 4d).

Biogeographical affinities

Our Central and South Namib (B) is the most distinct province, in that its closest point to its nearest neighbour is the farthest for any of the provinces (Fig. 3). Its closest neighbour, and therefore its closest affinities, could be with the Succulent West Coast Karoo (D2). Our Northern Namib (A) also has no very close affinities; the closest being with the Eastern Botswana Mopane subprovince (E4). It is surprising that the two provinces (Northern Namib and Central and South Namib) are quite so dissimilar, when geographically they lie adjacent to each other. The Kalahari (C) has strongest affinities with the Eastern Botswana Mopane (E4) and Thorn Tree Bushveld

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FIG. 4

The proposed phytochorology compared to published phytochorologies. (a) Provinces (A–F) and subprovinces (1–9) found by cluster analysis and multi-dimensional scaling of the distribution of 1 362 tree species in southern Africa. The boundaries of the provinces and subprovinces are based on the individual distribution patterns of the 10 most characteristic species (see Appendix 1) being super-imposed on one another, and where intersections of 80 % or more occurred the intersection areas were enclosed in a continuous boundary. (b), (c) and (d) are redrawn maps of Werger's phytochorology (1976), White's phytochorology (1965, 1971), and Giess's phytochorology for South-West Africa/Namibia (1970) respectively. Each of these maps have our corresponding regions' names inserted to show the degree of compatibility. Names of the provinces and subprovinces:

A = Northern Namib, B = Central and South Namib, C = Kalahari, D = Karoo, E = Zambeziaca, F = Afro-montane and Coastal Forest,

D1 = Arid Karoo, D2 = Succulent West Coast Karoo, D3 = Lower Mixed Veld Karoo, D4 = False Upper Karoo with Mixed Grassland, E1 = Combretum Tree Savanna and Woodland, E2 = Thorn Tree Bushveld, E3 = Mixed Acacia Bushveld, E4 = Eastern Botswana Mopaneveld,

E5 = Matabele Tree Savanna and Woodland, E6 = Zambezian Mixed Tree Savanna and Forest, E7 = Zambezian Montane Forest, E8 = Mozambique Coastal Woodland and Savanna, E9 = Transvaal Mixed Bushveld,

F1 = Capensis Montane Forest and Fynbos, F2 = Afro-montane Forest and Alpine Veld, F3 = Coastal Forest and Thornveld.

(E2) subprovinces, respectively. The Karoo (D) and Zambeziaca (E) provinces tend to be closest together at the Thorn Tree Bushveld (E2) and Arid Karoo (D1) subprovinces. The Afro-montane and Coastal Forest (F) province seems to have greatest affinities with the Zambeziaca (E) province, the most similar subprovinces between them being the Zambezian Montane Forest (E7) and the Coastal Forest and Thornveld (F3). This might be expected, since these areas experience similar temperature and rainfall regimes.

Southern Africa probably was covered by savanna and Cape sclerophyllous vegetation during the early Neogene (Axelrod and Raven, 1978). Alternating drought and wet periods are believed to have promoted enhanced plant speciation, in that during moist periods the sclerophyllous vegetation expanded into the present-day Karoo and speciated rapidly, whereas a coastward retraction occurred during dry conditions, leaving relict stands in the Karoo (Axelrod and Raven, 1978). Thus, relatively close affinities between the Karoo and Capensis might be expected. However, our Capensis Montane Forest and Fynbos (F1) subprovince is closest to the coastal forest and Thornveld (F3), and the whole of the Afro-montane and coastal Forest (F) province has affinities with a savanna, rather than a Karoo system (Fig. 3). Perhaps the onset of a dry climate and the forming of a Karoo system in its present position selectively excluded many trees, as opposed to relatively short-lived plants better able to escape the extremes of droughts. On this basis, it seems that our Karoo (D) province, with its dissimilar dominant species, represents a combination of the more xerophytic elements of the postulated former savanna and Cape sclerophyllous vegetation types.

During the Miocene the climate progressively became drier, restricting forest, while new vegetation forms, such as thorn scrub and grassland developed and savanna spread. Figure 3 shows that the Transvaal Mixed Bushveld (E9) subprovince has closer affinities with the Thorn Tree Bushveld (E2) than with its neighbouring Eastern Botswana Mopaneveld (E4). It seems likely that with increasing aridity the formerly continuous savanna between these two areas (E2 and E9) split, with the development of the Kalahari (C) in between and within the very dry interior basin.

A possible explanation of the dissimilarity between the adjacent Northern Namib (A) and Central South Namib (B) provinces might be that while the Northern Namib developed from the drier fringes of a tropical savanna, the Central South Namib developed at a later stage from the drier periphery of a then well-established Karoo system.

Species richness and environmental variables

Rainfall patterns for southern Africa demonstrate that the subcontinent is almost bisected by the 400 mm isohyet, with the eastern half considerably

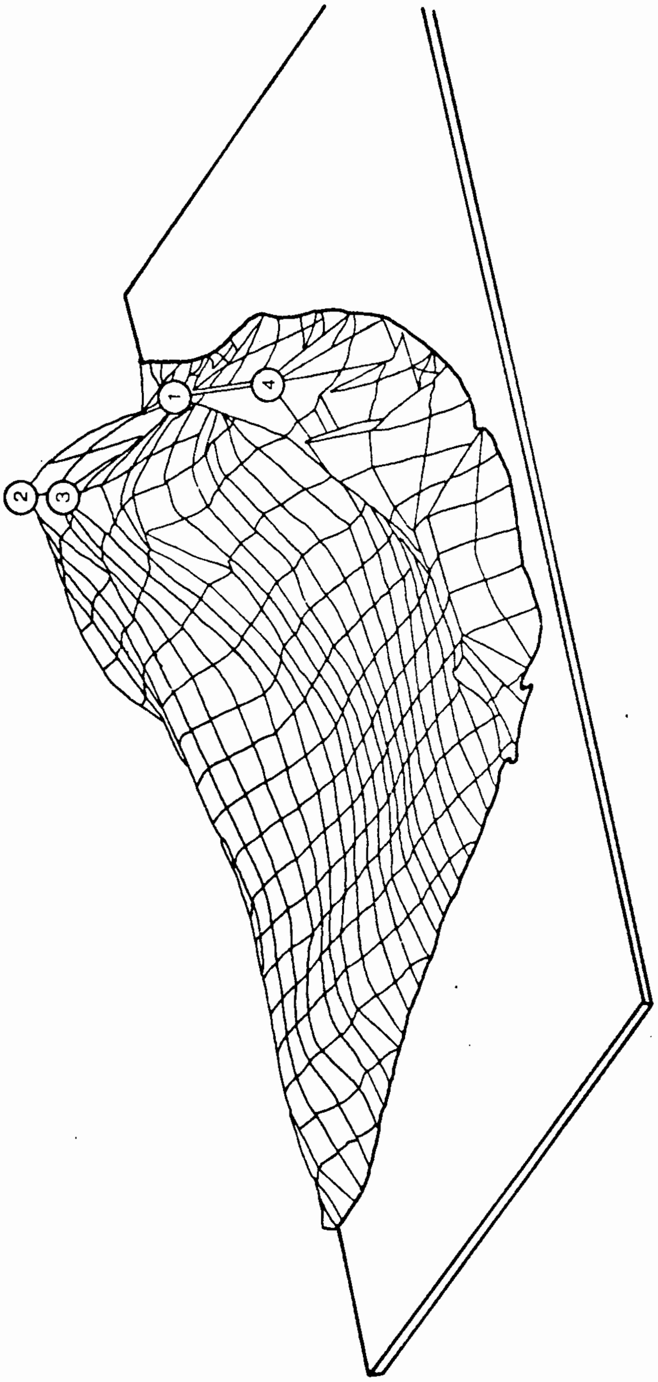

Fig. 5

Three-dimensional representation of the distribution of tree species richness in southern Africa (see Appendix 2). 1 = Komatipoort-Lebombo mountains (607 spp.), 2 = Vila Gouveia-Gorongosa (570 spp.), 3 = Haroni-Lusitu confluence (562 spp.), 4 = Zululand (554 spp.) are place names of areas with highest species richness.

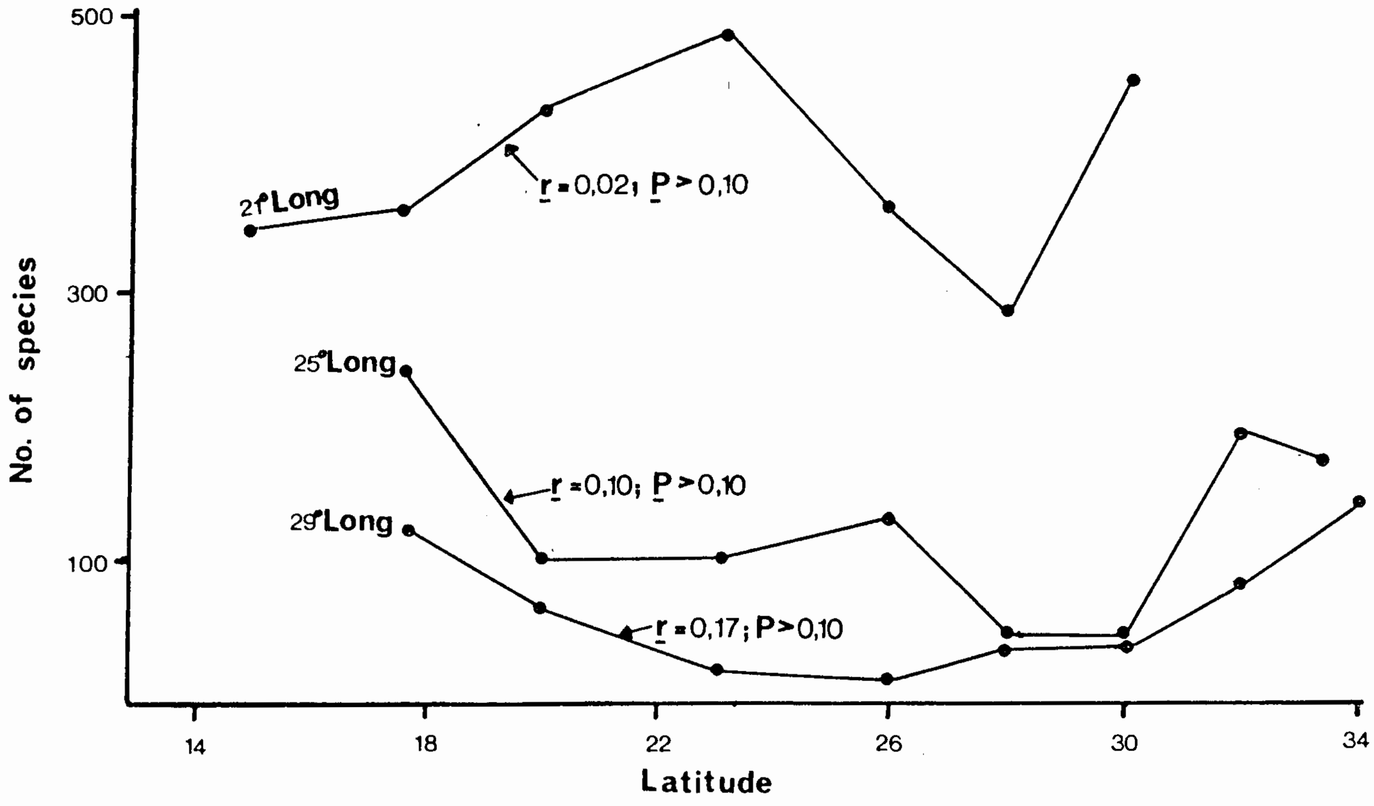

Fig. 6
Species richness of trees along three transects A–A1, B–B1 and C–C1 (see Fig. 1) in relation to latitude in southern Africa.

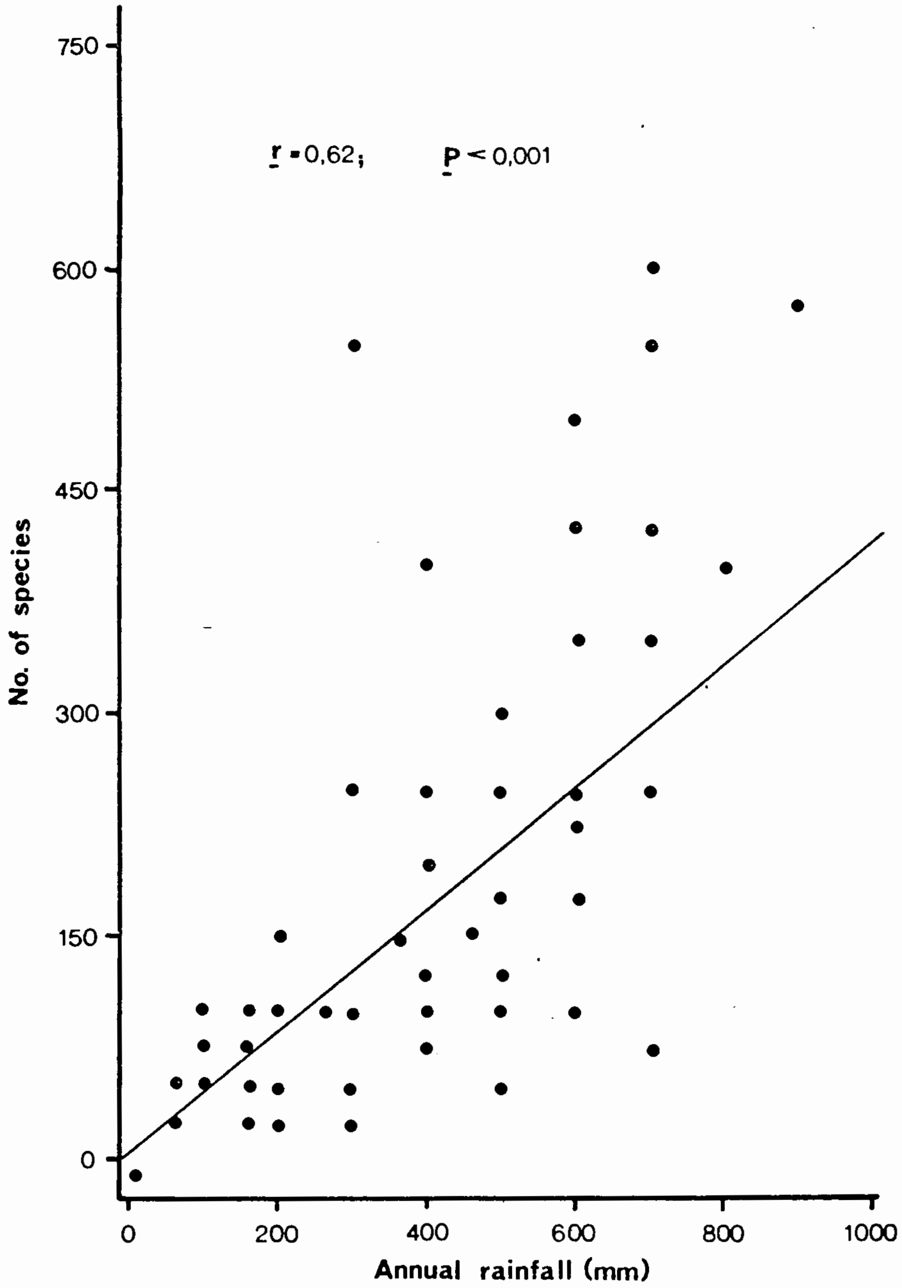

FIG. 7
Relationship between species richness of trees and mean annual rainfall in southern Africa.

moister than the western half (Jackson and Tyson, 1971). In general, tree species richness increases with increases in precipitation (Fig. 7), but it is probably more meaningful biologically to relate tree species richness to the extent of a positive difference between precipitation and water losses of the plants. Thus, a surprising result of our analyses is the low correlation between water surplus (WPLUS) and species richness (Table 1).

The intercorrelation between incoming solar radiation, temperature and precipitation, helps to explain why altitude range (ARANGE) has the second highest coefficient of determination in the multiple linear regression analysis (Table 1). In the stepwise regression analysis, only environmental variables which are not significantly correlated with those already in the regression equation can contribute to the regression (Allen, 1973). Thus, correlation and stepwise regression analysis are complementary statistical approaches (Crowe, 1979).

The most significant feature to emerge from the multiple characterization of each of our phytochorological provinces and subprovinces by environmental variables is that, areas with complex environments are not necessarily supportive of relatively high species richness. For instance, the Northern Namib province has great variability in temperature, rainfall and altitude, but the general aridity of the area apparently limits tree diversity, whereas other areas with less environmental diversity but higher rainfall support more species of trees.

Tropical biotas are thought to evolve and diversify relatively rapidly, because the tropics are less subject to widespread catastrophic events (e.g. glaciation) than temperate regions. On the other hand, the more heterogeneous and complex the physical environment becomes the more complex, and hence diverse, the biota becomes. The tropics are thought to be relatively heterogeneous and, therefore, to support more species than temperate regions. Thus, in essence, there are two lines of thought for explaining enhanced species richness in the tropics; and, they can be termed the "stability" and "heterogeneity" hypotheses, respectively.

If most of the variation in the species richness of the southern African tree flora could be linked with a combination of significant environmental variables, it could indicate subjectively a favouring of the "heterogeneity" hypothesis. For this to operate, the multiple regression analysis should have a high R^2 value (e.g. 0,85 or more). If, on the other hand, the variation in tree species richness is not only a function of present-day environmental variation, we would expect a much lower R^2 value (e.g. less than 0,66). We would interpret such a result to be consistent with a "stability" hypotheses, especially if the R^2 value was less than 0,50. Since the R^2 in the present study is 0,63, the most likely hypothesis is a mixed one. In other words, both environmental heterogeneity and stability have contributed to the observed

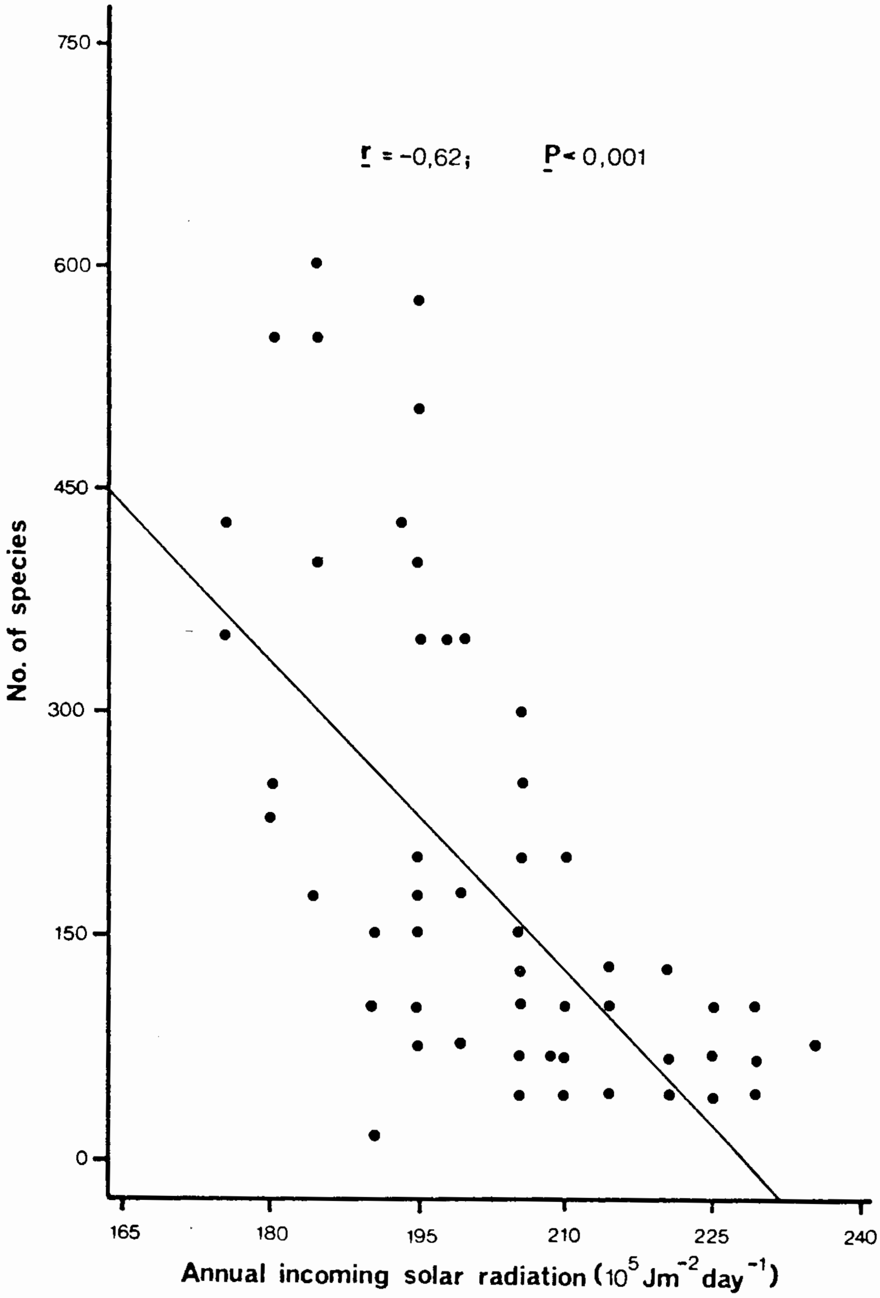

FIG. 8
Relationship between species richness of trees and mean annual solar radiation in southern Africa.

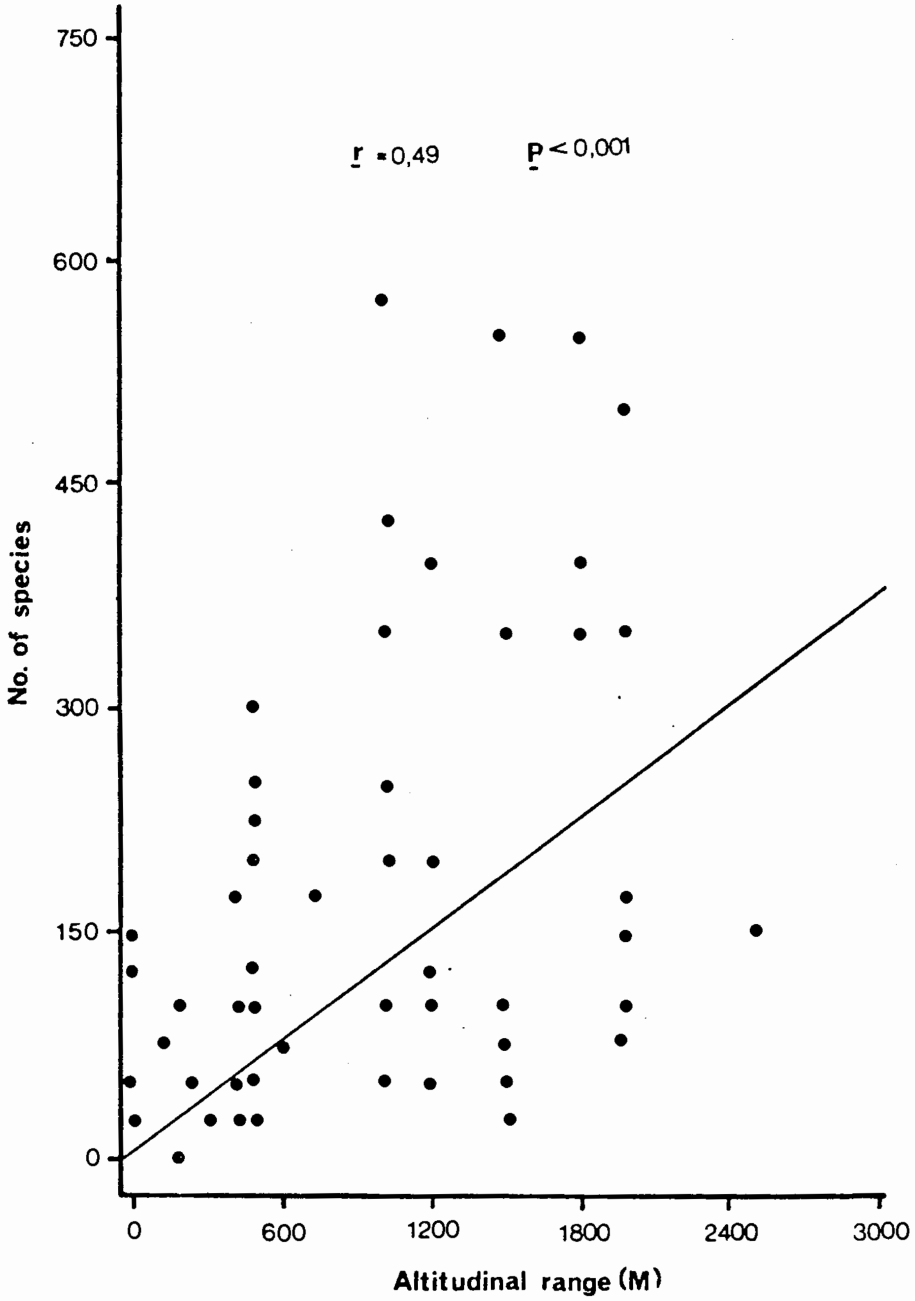

FIG. 9
Relationship between species richness of trees and altitudinal range in southern Africa.

patterns of diversity. Moreover, those quadrats which have far more species than their present-day environmental heterogeneity would predict (e.g. quadrats 15, 26, 35 and 55; Figs 1 & 5 and Appendix 2) are, by inference, the most likely centres of stability. We predict that these centres of stability could have been "refugia" sensu Simpson and Haffer (1978).

Accepting that the subcontinent has been changing from a wet regime to a drier one, it is logical that the last areas to be directly affected would be protected gorges on the windward side of mountains. It is only in these areas that sufficient moisture can be retained for the support of past, "super-saturated", climax communities of trees, and therefore have an observed high species richness. Moreover, these communities are located in areas of high habitat diversity and thus would tend to conform to the "heterogeneity" hypothesis as well.

All four areas of exceptionally high species richness (Fig. 5) are characterized by a high diversity of habitat types. The Komatipoort area includes the moist, windward side of the Lebombo mountains and the southern Mozambique coastal plain, as well as the drier leeward side of the Lebombo range. The Vila Gouveia area includes the Gorongoza and Amatonga forests in the east, and well developed gallery forests along the streams of the Manica platform. East of Inyanga there are large Afro-montane forests and to the west a dominant moist deciduous woodland *(Brachystegia)* prevails. The Chipinga-Espungabera is the site of the Haroni-Lusita confluence and the steep descent of the Chimanimani mountains. It is here that high-altitude montane and high and low-altitude deciduous and riparian forests exist, as well as dry gallery forest along the Sabi river. Such a wide range of forest types within relatively small areas can be expected to yield high levels of richness in tree species.

CONCLUSIONS

This report shows that meaningful phytochorological results can be achieved through study of the distribution of tree species in southern Africa, using modern quantitative methods. The derived phytochorology has a great deal of compatibility with schemes based on subjective decisions and qualitative information. We propose a two-tier classification for assemblages of tree species, and suggest that some of the relationships between assemblages are the result of changes in vegetation patterns in the past. Evidence for tree species richness increasing with decreasing geographical latitude is not encouraging, whereas an hypothesis for an expected decrease in species richness with increasing aridity is acceptable. Apparently the balance between water input, in the form of rainfall, and water losses, linked with high solar radiation and temperature levels, is a critical factor determining the number of tree species in any given area. The sum of the environmental variables studied cannot, however, adequately explain species richness variability and, therefore, other environmental factors that are not readily quantifiable (e.g., wind conditions), and/or historical factors, must be operating.

The results of our study apparently confirm Strahler's (1978) assertion that, "species groups tended not to be just groups with similar environmental preferences, but distinctive associations as well, with significance beyond their relationships to a particular site factor".

ACKNOWLEDGEMENTS

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APPENDIX 1

The 10 most characteristic ($P < 0{,}01$) tree species for each province and subprovince in southern Africa according to the information statistic test. Where there are fewer than 10 species for a province or a subprovince all the characteristic species are included.

Province A, Northern Namib

Species	2ΔI Value
Commiphora wildii	90,00
Welwitschia mirabilis	70,49
Commiphora tenuipetiolata	47,19
Commiphora multijuga	37,10
Boscia tomentosa	35,55

Province A, Northern Namib

Species	2ΔI Value
Commiphora anacardiifolia	29,51
Commiphora kraeuseliana	22,99
Entandrophragma spicatum	22,99
Euphorbia eduardoi	21,33
Combretum wattii	20,44

Province B, Central and South Namib

Species	2ΔI Value
Parkinsonia africana	55,71
Ozoroa concolor	21,98
Cyphostemma bainesii	15,73
Tammarix usneoides	7,27
Rhus viminalis	7,24
Rauvolfia caffra	5,93
Pterocarpus rotundifolius	5,60
Commiphora capensis	4,68
Commiphora saxicola	4,68

Province C, Kalahari

Species	2ΔI Value
Ehretia rigida	56,35
Rhigozum brevispinosum	27,82
Ozoroa paniculosa	17,61
Combretum collinum	15,14
Acacia haematoxylon	12,15
Grewia flava	10,20
Catophractes alexandri	8,95
Acacia nebrownii	5,49

Province D, Karoo

Species	2ΔI Value
Nymania capensis	192,50
Rhus viminalis	163,10
Salix mucronata	153,51
Rhus undulata	148,17
Ozoroa dispar	147,88
Salsola aphylla	124,04
Maytenus linearis	111,75
Acacia haematoxylon	102,38
Cadaba aphylla	91,34
Aloe comosa	88,46

Province E, Zambeziaca

Species	2ΔI Value
Combretum imberbe	238,00
Burkea africana	235,26
Combretum hereroense	219,51
Peltophorum africanum	208,02
Securinega virosa	202,94
Dombeya rotundifolia	195,59
Commiphora africana	191,35
Combretum apiculatum	184,09
Piliostigma thonningii	175,83
Adansonia digitata	171,90

Province F, Afro-montane and Coastal Forest

Species	2ΔI Value
Rhus erosa	256,88
Clutia pulchella	249,77
Scolopia mundii	243,26
Scutia myrtina	228,07
Cassine peragua	223,65
Galpinia transvaalica	214,74
Rapanea melanophloeos	214,56
Maytenus acuminata	210,59
Chrysanthemoides monilifera	206,35
Burchellia bubalina	204,81

Subprovince D1, Arid Karoo

Species	2ΔI Value
Acacia haematoxylon	64,03
Boscia foetida	53,32
Aloe comosa	35,33
Adenolobus garipensis	23,29
Ozoroa namaensis	22,63
Acacia erioloba	22,35
Rhigozum brevispinosum	21,32
Salsola aphylla	20,81
Nymania capensis	20,07
Aloe littoralis	18,85

Subprovince D2, Succulent West Coast Karoo

Species	2ΔI Value
Aloe ramosissima	45,33
Ozoroa concolor	28,33
Euclea racemosa	21,90
Dideltia spinosa	20,22
Maerua gilgii	19,90

Subprovince D2, Succulent West Coast Karoo

Species	2ΔI Value
Euphorbia guerichiana	18,09
Ozoroa crassinervia	16,89
Aloe pillansii	15,27
Pachypodium namaquanum	14,04
Cotyledon paniculata	8,03

Subprovince D3, Lower Mixed Veld Karoo

Species	2ΔI Value
Chrysanthemoides monilifera	41,69
Dodonaea viscosa	38,62
Buddleja glomerata	38,62
Protea arborea	32,18
Phylica oleifolia	32,18
Phylica villosa	32,18
Rhus tomentosa	28,97
Hartogia schinoides	28,97
Kiggelaria africana	27,74
Diospyros glabra	25,75

Subprovince D4, False Upper Karoo with Mixed Grassland

Species	2ΔI Value
Rhus leptodictya	48,65
Euclea crispa	48,63
Ilex mitis	47,33
Ficus soldanella	46,87
Protea caffra	46,87
Celtis africana	44,95
Cussonia paniculata	43,52
Carissa bispinosa	43,52
Diospyros whyteana	41,28
Rhus pyroides	40,27

Subprovince E1, Combretum Tree Savanna and Woodland

Species	2ΔI Value
Grewia schinzii	96,79
Combretum engleri	65,24
Ozoroa longipes	61,35
Combretum psidioides	49,96
Combretum celastroides	46,77
Steganotaenia araliacea	43,23
Pachypodium lealii	42,72
Bridelia tenuifolia	38,91
Bauhinia urbaniana	35,02
Entandrophragma spicatum	35,02

Subprovince E2, Thorn Tree Bushveld

Species	2ΔI Value
Ozoroa crassinervia	110,57
Moringa ovalifolia	95,43
Euclea pseudebenus	90,20
Cyphostemma currorii	83,82
Ficus cordata	77,73
Boscia foetida	77,73
Ficus ilicina	74,08
Montinia caryophyllacea	73,74
Vernonia cinerascens	72,98
Commiphora tenuipetiolata	69,92

Subprovince E3, Acacia Bushveld

Species	2ΔI Value
Lonchocarpus nelsii	26,09
Acacia fleckii	24,98
Grewia retinervis	15,99
Combretum collinum	15,52
Catophractes alexandri	13,28
Commiphora angolensis	11,49
Rhus tenuinervis	9,98
Commiphora africana	7,28
Bauhinia petersiana	6,84
Hibiscus diversifolius	4,91

Subprovince E4, Eastern Botswana Mopane

Species	2ΔI Value
Colophospermum mopane	9,77
Catophractes alexandri	8,45
Albizia harveyi	5,82
Grewia tenax	4,78
Hyphaene benguellensis	4,53
Acacia nebrownii	4,15

Subprovince E5, Matabele Savanna and Woodland

Species	2ΔI Value
Vepris zambesiaca	119,81
Cassia singueana	111,33
Euphorbia matabelensis	108,60
Boscia angustifolia	99,85
Azanza garckeana	97,72
Combretum elaeagnoides	94,79
Commiphora mossambicensis	92,63
Elephantorrhiza goetzei	85,47
Dalbergia melanoxylon	76,65
Pterocarpus rotundifolius	76,28

Subprovince E6, Zambezian Mixed Tree Savanna and Forest

Species	2ΔI Value
Rhodognaphalon schumannianum	22,89
Triplochiton zambesiacus	20,48
Schrebera trichoclada	14,96
Leptactina hexamera	11,44
Diospyros squarrosa	10,60
Tamarindus indica	10,57
Monotes engleri	10,10
Uapaca nitida	9,52
Cola mossambicensis	9,43
Allophylus africanus	8,37

Subprovince E7, Zambezian Montane Forest

Species	2ΔI Value
Cassia petersiana	66,12
Acacia xanthophloea	61,50
Androstachys johnsonni	58,20
Stadmania oppositifolia	56,84
Breonadia microcephala	53,73
Strychnos mellodora	49,13
Xeromphis rudis	47,98
Rinorea elliptica	47,34
Trichilia emetica	46,71
Thilachium africanum	46,60

Subprovince E8, Mozambique Coastal Woodland and Savanna

Species	2ΔI Value
Casearia gladiiformis	85,22
Enterospermum littorale	78,62
Coffea racemosa	69,86
Diospyros rotundifolia	68,78
Drypetes natalensis	66,09
Pseudobersama mossambicensis	63,87
Tarenna junodii	63,79
Ochna natalita	60,50
Sonneratia alba	58,96
Avicennia marina	58,96
Barringtonia racemosa	58,96

Subprovince E9, Transvaal Mixed Bushveld

Species	2ΔI Value
Buddleja saligna	115,33
Aloe marlothii	114,70

Subprovince E9, Transvaal Mixed Bushveld

Species	2ΔI Value
Acacia caffra	112,42
Commiphora neglecta	106,17
Solanum giganteum	100,84
Berchemia zeyheri	100,35
Nuxia congesta	92,59
Canthium suberosum	89,51
Cussonia paniculata	87,39
Protea caffra	85,62

Subprovince F1, Capensis Montane Forest and Fynbos

Species	2ΔI Value
Rhus incisa	72,23
Atalaya capensis	72,23
Cassine parvifolia	67,42
Freylinia lanceolata	65,01
Lachnostylis hirta	62,60
Hartogia schinoides	58,70
Maytenus oleoides	57,79
Protea arborea	57,79
Euclea racemosa	50,10
Olea exasperata	49,85

Subprovince F2, Afro-montane Forest and Alpine Veld

Species	2ΔI Value
Rhus transvaalensis	73,46
Rhus erosa	37,57
Calpurnia robinioides	28,89
Rhus montana	21,67
Protea caffra	19,26
Euphorbia curvirama	12,04
Euclea coriacea	11,97
Leucosidea sericea	9,15
Cussonia paniculata	8,90
Erica caffrorum	8,84

Subprovince F3, Coastal Forest and Thornveld

Species	2ΔI Value
Vitellariopsis marginata	58,64
Dombeya cymosa	54,97
Turraea floribunda	54,97
Euphorbia tirucalli	54,24
Brachylaena ilicifolia	51,31
Bersama lucens	51,31

Subprovince F3, Coastal Forest and Thornveld

Species	2ΔI Value
Nuxia congesta	50,70
Tricalysia capensis	48,93
Cussonia sphaerocephala	47,64
Diospyros villosa	47,64

APPENDIX 2

The number of tree species in the quadrats shown in Fig. 1.

No.	Spp.	No.	Spp.	No.	Spp.	No.	Spp.	No.	Spp.
1	242	15	570	29	93	43	117	57	59
2	342	16	355	30	46	44	180	58	44
3	409	17	20	31	26	45	349	59	33
4	181	18	112	32	13	46	607	60	51
5	1*	19	109	33	96	47	25	61	95
6	90	20	57	34	209	48	60	62	49
7	142	21	62	35	494	49	53	63	74
8	126	22	103	36	395	50	41	64	65
9	121	23	96	37	233	51	41	65	94
10	113	24	238	38	27	52	55	66	202
11	189	25	434	39	63	53	85	67	359
12	238	26	562	40	31	54	258	68	148
13	295	27	251	41	13	55	554	69	160
14	352	28	95	42	30	56	44	70	187

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* Excluded from the multivariate analysis as most of it fell outside the range of the maps used in Coates Palgrave.

NOTES ON THE DATA SOURCE AND COLLECTION

Tree distributions

Coates Palgrave (1977) distribution maps which were updated in 1982 were used. These maps were prepared from official records lodged in the herbaria at Pretoria, Cape Town, Durban and Harare. There is no doubt that species occurring outside the area shown on these maps are possible, while not all areas within the distributions possess the species.

The choice of 70 quadrats, although may have seemed high for the Coates Palgrave maps, it is unlikely that this exceeded the accuracy of the data base (E.J. Moll pers. comm.). Further, this grid size facilitated the collection of environmental data. Most of this data was extracted from Thornthwaite (1962) and the 70 quadrat grid allowed most quadrats a minimum of five meteorological stations. A few quadrats had fewer than this number and therefore other information such as Jackson (1971) Climatological Atlas was used. If these quadrats were made larger the mean climatic values representing these quadrats would become increasingly meaningless.

Each of these quadrats are not of a uniform size due to the constraints of the climatological data and irregular coastlines. The mean quadrat size, however, corresponds to an actual measurement of 200 km by 200 km. Since the information was digitalized for each of the 70 quadrats on the basis of cover, 1 = 10% of the quadrat being covered by the distribution, 2 = 20% coverage etc. variations in quadrat size are not critical. Had a presence/absence criteria been used equal area quadrats would have been critical.

Rationale for selection of environmental variables.

Radiation is important in plant production as it constitutes the primary source of energy; however, once a threshold amount of radiation is achieved, additional quantities are of no usefulness, and may in fact have negative effects. With excessively high radiation rapid transpiration rate are stimulated, which necessitates extra amounts of water to stave off wilting. Overall the sub-continent has very high radiation values (Thornthwaite 1962), and due to the extra water stress imposed on the plants by high radiation values it would be expected to have a negative correlation between the plant species richness and the radiation. Mean values are, however, not necessarily the most strongly correlated and maxima and minima are also very important agents in controlling distribution. Radiation values for any time period may exceed the plant's built-in tolerance levels and effectively exclude that particular plant from that area. Winter and summer values (mean, maximum and minimum) were also investigated to accommodate seasonal changes which could effectively exclude species from particular areas. Range in solar radiation is in fact the spatial range between these minimum and maximum values, and is included to allow for environmental variation.

Temperature is undoubtedly very important in its effects on plant distribution. Plants, unlike animals, are unable to escape from temperature (and radiation) effects and are therefore sensitive to variations. Mean temperature is included by convention, while the maximum value for January is taken to indicate the maximum temperature that may occurr; in order to survive the plant must accommodate these temperatures. Similarly plants are also very susceptible to cold temperatures (which are able to inflict tissue damage) and therefor the lowest June values are included. Mean values for January and July are included in order to accommodate seasonality. Some plants may be able to endure short term extremes, but are unable to withstand prolonged conditions and thus may be excluded from an area. The range of temperature is to allow for spatial variations in the environment. Rainfall is considered to be one of the strongest factors in determining the nature of vegetation (Kellman 1975). All plants are dependent on water for continued photosynthesis processes. Southern Africa on the whole tends to experience too little rainfall for the maintenance of many plant communities. Seasonality of rainfall is critical, as transpiration and photosynthesis are continually operating and therefore necessitates a steady water source. Shortage of water in any season may eliminate many plant species, and rainfall range is also included to allow habitat diversities. Out of these relationship water balance values have been derived, which in the view of Thornthwaite (1962) are more meaningful as they indicate available water for the plant rather than just a total. These values are worked out by comparing potential evaporation and actual rainfall. Altitude is important in that a greater range of height within the quadrat would possibly produce more habitats and therefore a greater species richness.

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