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Inter-island floristic similarities in the Macaronesian region

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Abstract

Macaronesia was recognized as a biogeographical region more than a century ago. However, this concept has been recently criticized due to the floristic heterogeneity of the region.

This paper analyzes and interprets the inter-island floristic similarities using presence-absence data for 30 islands and 3114 phanerogamous species. Agglomerative classification, method UPGMA, and Principal Coordinates Analysis were applied.

The results show a close correlation between variation in floristic similarities and latitude, altitude and distance from the continent. These correlations are interpreted in relation to the variation in climatic conditions, the possibility of long-distance dispersion and island size.

We conclude that the selective effect of climate and opportunity for long-distance dispersion are the primary factors explaining the present inter-island floristic variation.

Introduction

The inclusion of the Açores archipelago, Madeira and Selvagens Islands, Canary Islands and Cape Verde Islands in the Macaronesia biogeographic region has been generally accepted for over a century (Sunding 1979; Lobin 1982). This region includes 30 islands which differ in latitude, altitude, area and distance from the continent (Table 1).

Some authors have recently highlighted the floristic heterogeneity within the region (Sunding 1979; Santos 1983) and questioned its unity as a biogeographic region (Lobin 1982).

The more traditional approach to this problem emphasizes the historical spatial or temporal discontinuity to explain the actual pattern of the vegetation (Sunding 1979). However other argue for an alternative approach, based on several facts: the islands are younger than was previously thought (Abdel Monen *et al.* 1972) and the African, European and American continents had already become separated by the time these islands were formed; limitations of long-distance dispersion may be less than has been generally assumed, due to the proximity of the trade winds, and the prevailing N-S marine current around the Canary Islands (Bramwell 1985); and regular volcanic activity created new land to be colonized by new species. Furthermore, the continental biogeographical pattern between present vegetation and climatic factors show a closely relationship (Quézel 1978).

On the other hand, (i) the high proportion of Macaronesian species which also occur in the Mediterranean region (Sunding 1979), (ii) the similarity between some endemic Macaronesian species and equivalent Mediterranean species

Table 1. Macaronesian islands listed by archipelago. The Selvagens Islands are included in the Madeira archipelago. Longitude (Long.) and latitude (Lat.) in degrees, altitude (Alt.) in m., area in km^2., distance from the continent (Dist.) in Km. and number of vascular species (N. sp.) are indicated.

N.	Key	Name	Long.	Lat.	Alt.	Area	Dist.	N. sp.
		Açores						
1	S	Santa Maria	25.1	36.9	587	97	1588	423
2	M	San Miguel	25.5	37.7	1103	757	1584	685
3	T	Terceira	27.2	38.7	1021	401	1764	608
4	G	Graciosa	27.8	39.1	402	61	1844	279
5	J	San Jorge	27.9	38.7	1053	246	1832	422
6	P	Pico	28.2	38.5	2351	446	1860	508
7	F	Faial	28.5	38.6	1043	173	1908	578
8	L	Flores	30.9	39.4	914	143	2152	389
9	C	Corvo	30.8	39.7	718	17	2148	293
		Madeira						
10	M	Madeira	16.9	32.7	1861	728	668	1142
11	D	Desertas	16.4	32.5	184	10	640	176
12	P	Porto Santo	16.3	33.0	520	69	680	439
13	S	Selvagens	15.9	30.0	154	4	388	92
		Canary						
14	L	Lanzarote	13.6	29.0	671	796	132	593
15	F	Fuerteventura	14.1	28.3	807	1725	104	614
16	C	Gran Canaria	15.5	27.9	1950	1532	200	1289
17	T	Tenerife	16.6	28.2	3717	2058	292	1396
18	G	La Gomera	17.2	28.0	1487	378	340	801
19	H	El Hierro	17.9	27.6	1501	278	388	578
20	P	La Palma	17.1	28.6	2423	729	424	806
		Cape Verde (Barlovento)						
21	A	San Antao	25.2	17.0	1979	779	792	498
22	V	San Vicente	25.0	16.7	774	227	772	278
23	L	Santa Luzia	24.7	16.7	395	35	752	55
24	N	San Nicolau	24.2	16.5	1304	343	680	319
25	S	Sal	22.9	16.7	406	216	576	129
26	B	Boa Vista	22.8	16.0	390	620	540	188
		Cape Verde (Sotavento)						
27	M	Maio	23.1	15.2	436	269	560	154
28	T	San Thiago	23.5	15.0	1392	991	592	425
29	F	Fogo	24.3	14.9	2829	476	684	359
30	R	Brava	24.7	14.8	976	64	720	192

(Bramwell 1976; Humphries 1979) and (iii) the discovery of fossils with Macaronesian or South European vicariant species characteristics (Andreansky 1968; Ferguson 1974), suggest the existence of a Miocene Mediterranean dispersion centre, bordering the Tethys Sea, which may have extended through North Africa in the Pleistocene, during the glacial periods.

Furthermore, the occurrence of Macaronesian and vicarious species in the west, east and south

Table 2. Mean annual temperature (T) in °C degrees, mean annual precipitation (P) in mm and altitude (Alt.) in m for 24 meteorological stations in Macaronesia. Five nearby continental stations are added for comparison.

N.	Station	Island	Alt.	T.	P.
	Açores				
1	Ponta Delgada	San Miguel	22	17.3	697
2	Horta	Faial	61	17.4	1022
3	Angra do Heroismo	Terceira	31	17.2	953
4	Santa Cruz	Flores	40	17.5	1447
5	Achada das Furnas	San Miguel	550	13.2	1730
	Madeira				
6	Porto Santo	Porto Santo	45	19.0	338
7	Funchal	Madeira	25	18.3	645
8	Santo da Serra	Madeira	660	14.7	1783
9	Encumeada	Madeira	950	13.0	2675
	Canary				
10	Arrecife	Lanzarote	10	20.8	035
11	Santa Cruz	Tenerife	37	20.9	290
12	La Laguna	Tenerife	547	16.5	597
13	Aguamansa	Tenerife	1150	13.7	843
14	Santa Cruz	La Palma	20	20.3	439
15	Punta Orchilla	El Hierro	150	21.4	157
16	Las Palmas	Gran Canaria	12	20.6	243
	Cape Verde (Barlovento)				
17	Sal Rei	Boa Vista	16	21.9	091
18	Mindelo	San Vicente	4	23.5	117
19	Punta do Sol	San Antao	20	21.6	218
20	Preguica	San Nicolau	25	24.1	098
	Cape Verde (Sotavento)				
21	Praia	San Thiago	22	24.7	264
22	San Filipe	Fogo	80	25.1	181
23	V.Nova da Sintra	Brava	507	20.2	410
24	Monte Velha	Fogo	1299	18.9	1610
	Continental stations Station	Country			
25	Lisboa	Portugal	100	15.9	602
26	Safi	Marocco	15	19.5	397
27	Cabo Juby	Marocco	8	18.8	051
28	Nouakchott	Mauritania	5	25.8	121
29	Sant Louis	Senegal	3	24.1	381

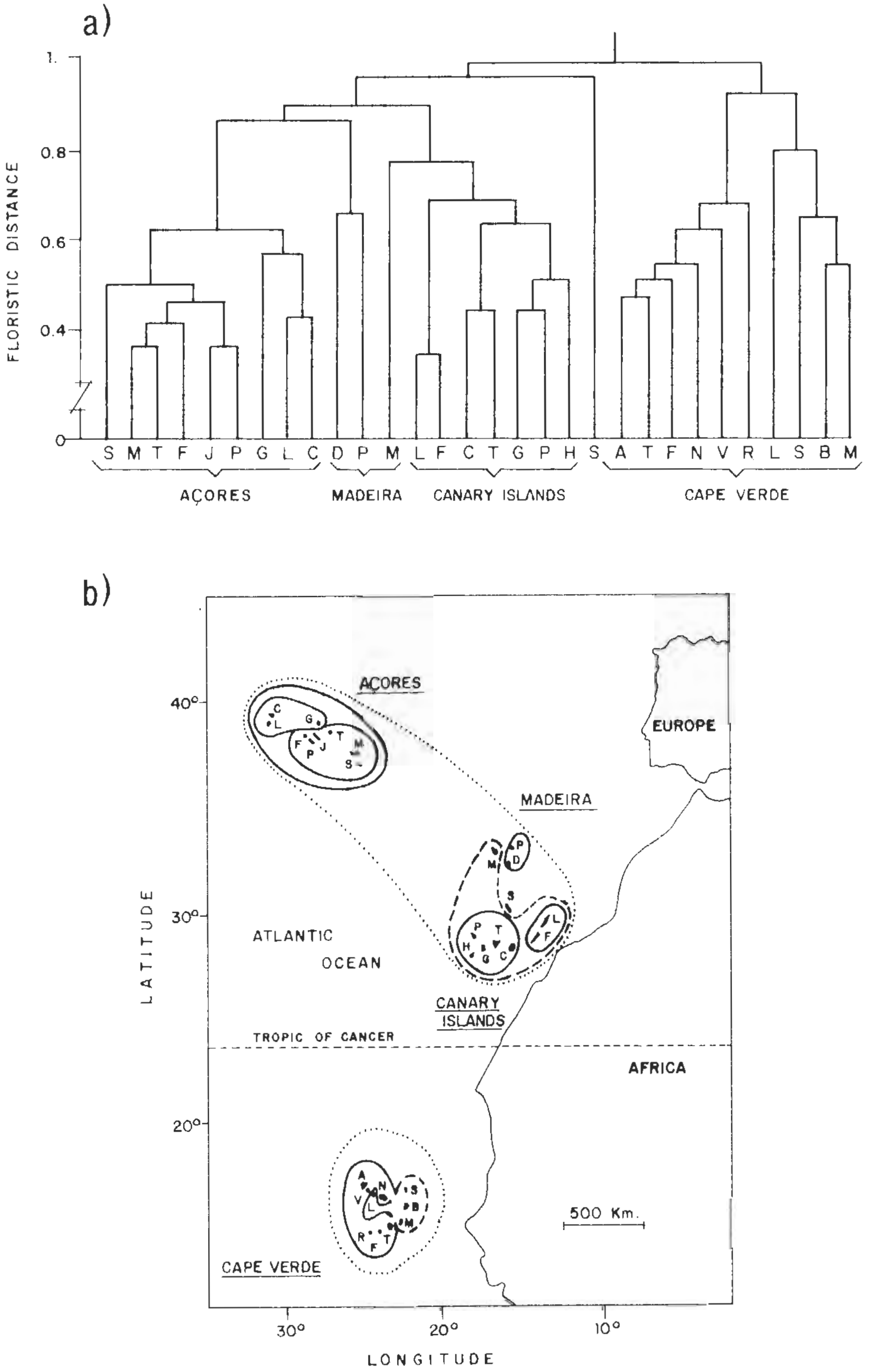

Fig. 1. (a) Dendrogram obtained by clustering of all 30 islands on the basis of inter-island dissimilarity (indicated as floristic distance in the dendrogram). See Table 1 for explanation of island symbols. The Cape Verde archipelago is the most differentiated of all groups, while the position of the Selvagens Islands is due to their small size. (b) Geographical position of the Macaronesian islands, and floristic grouping according to floristic dissimilarity, as shown in Fig. 1a. Three levels of similarity are indicated: —— >0.7, --- 0.7-0.8, ● ● ● 0.8-0.9.

of Africa, suggests the possibility of a tropical African dispersion centre. (Quézel 1978; Bramwell 1985). Both centres are important to explain the origin of the continental and Macaronesian archipelagos' vegetation. Its initial continuous dispersion area was later fragmented by the expansion of the desert. This fact would explain the large amount of fragmented distribution areas (Quézel 1978; Bramwell 1985).

Our general assumption is that the selection by climatic conditions, long-distance dispersion and island size (MacArthur & Wilson 1967; Adsersen 1988) are the primary factors that explain the present floristic variability. We also suggest that these factors have been continuously significant to the present. Furthermore, we predict a significant correlation between floristic, geographical and climatic variability. If we do not find any of these correlations significant, we have to emphasize the historical and geographical discontinuity between Macaronesia and the continent.

It has now become obvious that biogeographical problems of within- and between-similarities must be solved with quantitative methods (Crovello 1981; Lausi & Nimis 1985; Adsersen 1988; Andersson 1988). Sunding (1979) made a first attempt in this direction for the Macaronesian archipelagos, although no correlation between climatic conditions and floristic similarity was performed.

The present paper attempts to quantitatively describe the inter-island floristic variation in the Macaronesian region and its correlation with geographical conditions, variation in temperature and humidity, long-distance dispersion and island size.

Methods

Presence-absence data for 30 islands and 3114 vascular plant species, including introduced weeds, were compiled from a check-list of the Macaronesian flora (Hansen & Sunding 1985). The floristic dissimilarity for each pair of islands was calculated as $1 - J$, where J is Jaccard's index ($c/a + b - c$). This index can be rewritten as (c/s) where 's' is the total number of species on either island and 'c' the number of common species.

On the basis of this matrix, the agglomerative UPGMA classification method (Sokal & Michener 1958; Rohlf 1963), and Principal Coordinates Analysis (PCOOR: Gower 1966) ordination method were applied. The PCOOR results were interpreted by correlating the main floristic axes with latitude, distance from the continent, maximum altitude, precipitation and mean annual temperature of the islands.

Results and discussion

The UPGMA island grouping (Fig. 1) shows a close floristic similarity between nearby islands of the same archipelago despite differences in size and altitude (Table 1). The Cape Verde archipela-

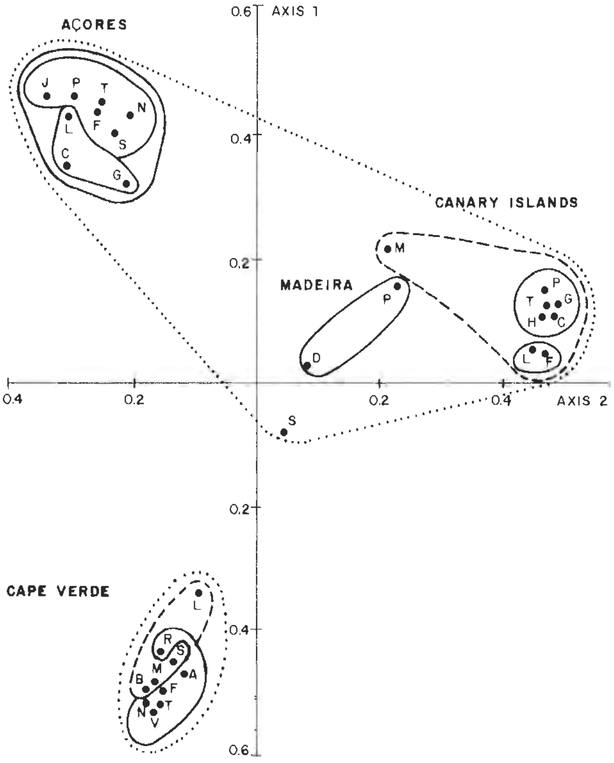

Fig. 2. PCOOR. Ordination of Macaronesian islands, axes 1 and 2. Floristic groupings are taken from the dendrogram presented in Fig. 1a.

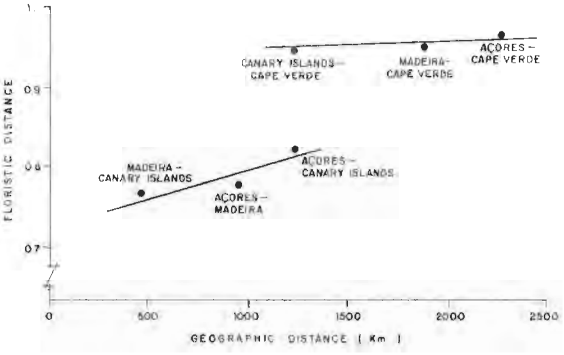

Fig. 3. Relation between average floristic distance and geographical distance among the Macaronesian archipelagos. Note, the high floristic distances with the Cape Verde archipelago.

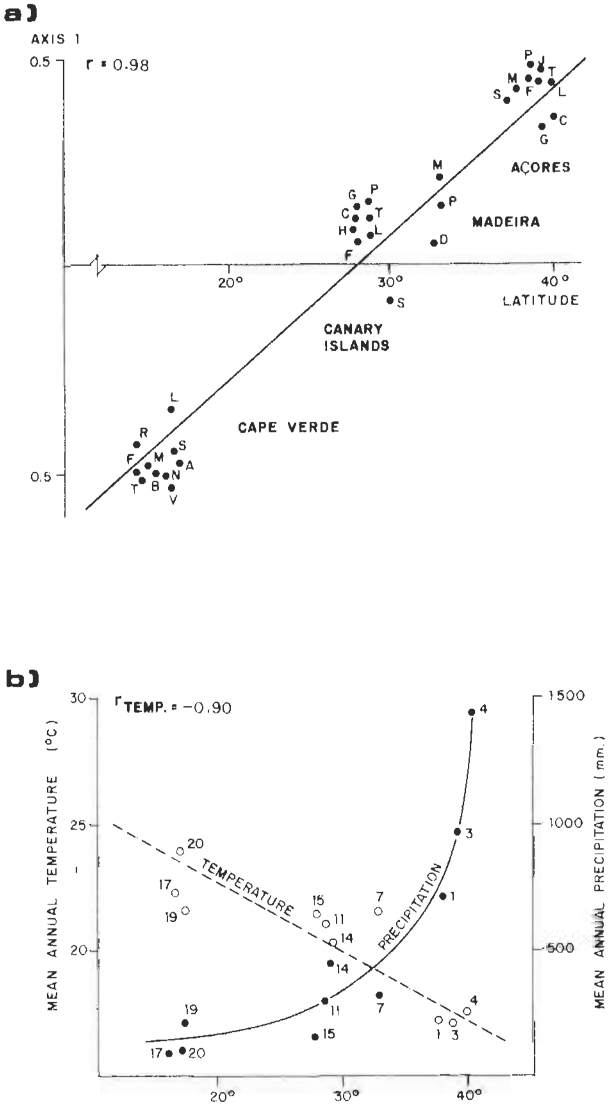

Fig. 4. (a) Correlation of PCOOR axis 1 position and latitude of each island. (b) Latitudinal variation of precipitation (black circles) and temperature (open circles) in Macaronesia. Only meteorological stations below 100 m altitude were included. Correlation with temperature is interpreted as lineal, precipitation as exponential.

go differs considerably from the others. The position of the Selvagens islands is not realistic because of the few species found there and the dissimilarity index chosen. Clearly, a different approach to similarity should be considered, e.g. an asymmetric coefficient or the probabilistic approach of Adsersen (1988).

As PCOOR axes 1 and 2 in the diagram show, the floristic distribution pattern is similar to the geographical one (Fig. 2).

The comparison between geographic distance among archipelagos versus mean floristic distance shows a gap between the variation pattern of Cape Verde Island and the other Macaronesian islands (Fig. 3). These results concur with the definition of Cape Verde as an independent Macaronesian subregion (Sunding 1979) or even as a Saharan-Sindian subregion (Lobin 1982).

Fig. 4a shows a high correlation between position along PCOOR axis 1 and latitude. This has been explained as a consequence of the latitudinal variations in precipitation and temperature (Fig. 4b), the variation in precipitation being exponential.

The position of the archipelagos along the second PCOOR axis is exponentially correlated to the distance from the continental coast (Fig. 5a). This complex pattern could be interpreted as being determined by both an increase in precipitation as the distance from the continental coast is increased (Fig. 5b), and the influence that may have the dispersion of continental species.

The third PCOOR axis distinguishes the islands according to their altitude when each archipelago is considered separately (Fig. 6a). The variation in the slope and the length of the

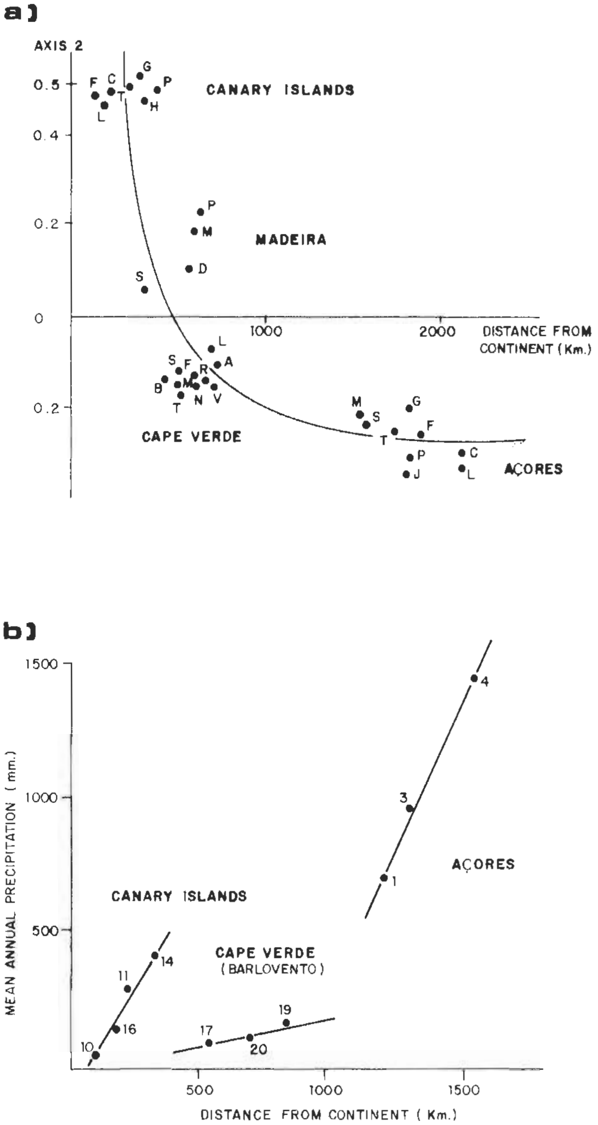

Fig. 5. (a) Correlation between coordinates of islands along PCOOR axis 2 and distance to the continent. (b) Correlation between precipitation and distance to the continental coast, presented separately for three groups of islands. Only meteorological stations below 110 m were included. The South Cape Verde islands, with an equatorial influence were excluded.

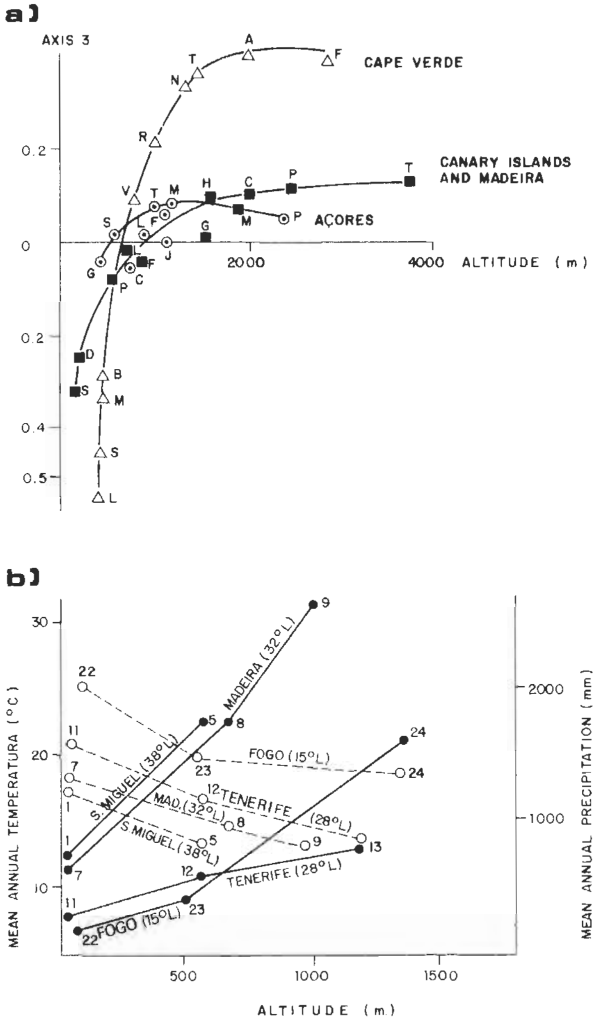

Fig. 6. (a) Axis 3 PCOOR position versus altitude of each island. Azores Islands (open circles), Canary Islands and Madeira (filled squares) and Cape Verde Islands (open triangles). The Madeira and Canary Islands were taken together. Beyond a certain altitude, the coordinates for this axis get stabilized. The gradient of each curve increases with latitude. (b) Temperature variation (open circles and broken lines) and precipitation variation (filled circles and continuous lines) according to altitude. The parallel displacement of both types of lines according to latitude is due to latitudinal climatic differences. The floristic information represented by axis 3 is associated with the altitudinal climatic gradient of each island.

curves is related to the latitude. This third PCOOR axis can be attributed to the effect of the altitudinal climatic gradient on the floristic inter-islands differentiation (Fig. 6b). Larger and higher islands have a greater environmental diversity than the smaller and lower ones. The differentiation in bioclimatic belts increases as the islands are nearer to the Equator.

On the plane defined by the first and third PCOOR axis (Fig. 7), when each archipelago is considered separately, the maximum variation line is associated with a combination of both PCOOR axis; the maximum variation being between smaller and lower islands and larger and higher ones. The slope and the length variation lines are evidence of a progressive increase in the significance of altitude when approaching the Equator.

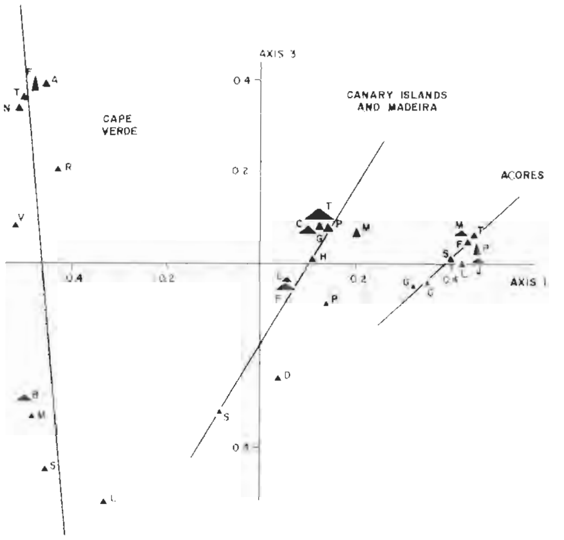

Fig. 7. Position of the islands in the plane defined by axes 1 and 3 PCOOR. Each island is represented by a triangle with base and height proportional to area and altitude respectively. Taking the archipelagos separately, axes 1 and 3 seem to be positively correlated. The difference between low and high islands increases toward the Equator.

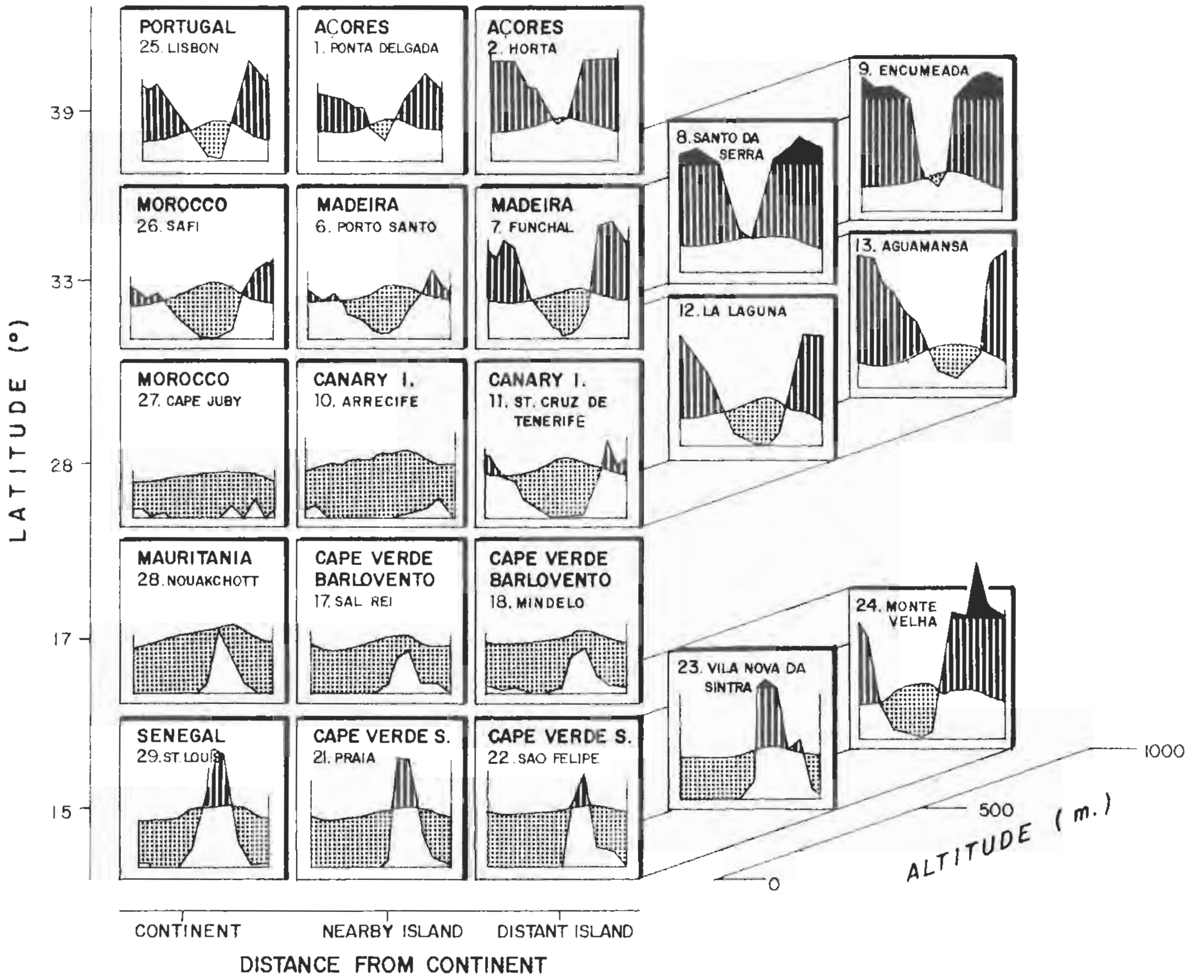

Fig. 8. Geographical components of climatic variation in Macaronesia. The temperature decreases with latitude and altitude. Precipitation increases with latitude and altitude and is positively correlated with distance from the coast. Data from Kämmer (1974) and Walter & Lieth (1967).

The floristic variation components (PCOOR axes 1, 2, 3) are related to typical geographical parameters (latitude, longitude and altitude) because they are ortogonal factors which explain the principal bioclimatic variation components, as shown in Fig. 8.

The close correlation between inter-island floristic variation and climatic conditions is supported by results obtained in other areas where no dispersion problems occur (Lausi & Nimis 1985). Furthermore, it is assumed that this vegetation is in equilibrium with its environment and that the selective effect of climate and the long-distance dispersion possibility are the primary factors which explain the present vegetation distribution.

As a null hypothesis, it may be assumed likely to encounter a continuous variation pattern between Macaronesia and the continent, and that the present vegetation results from a dynamic interchange with continental vegetation. But, to test this hypothesis it would be necessary to carry out a new analysis with continental samples included. Furthermore, it would be advantageous to differentiate among several altitudes in order to discriminate between climatic and long-distance dispersion factors on the floristic variation. Nevertheless, some differences may subsist from continuity due to the effect of long-distance dispersion and the particular evolution of insular species.

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References

Abdel Monen, A., Watkins, N. D. & Gast, P. W. 1972. Potassium Argon ages, volcanic stratigraphy and geomagnetic polarity history of the Canary Islands: Tenerife, La Palma and Hierro. Am. J. Soil Sci. 272: 805–525.

Adsersen, H. 1988. Null hypotheses and species composition in the Galápagos Islands. In: During, H. J. *et al.* (eds), Diversity and pattern in plant communities, pp. 37–46. Academic Publishing, The Hague.

Andersson, P. 1988. Ordination and classification of operational geographic units in Southwest Sweden. Vegetatio 74: 95–106.

Andreanszky, G. 1968. Neue und interessante terziäre Pflanzenarten aus Ungarn. Acta Bot. Acad. Scient. Hung. 14: 219–242.

Bramwell, D. 1976. The endemic flora of the Canary Islands; distribution, relationships and phytogeography. In: Kunkel, G. (ed.), Biogeography and ecology of the Canary Islands, pp. 207–240. Junk, The Hague.

Bramwell, D. 1985. Contribución a la biogeografia de las Islas Canarias. Botánica Macaronésica, 14: 3–34.

Crovello, J. J. 1981. Quantitative biogeography: An overview. Taxon, 30: 563–575.

Ferguson, D. K. 1974. On the taxonomy of recent and fossil species of *Laurus* (Lauraceae). Bot. J. Linn. Soc. 68: 51–72.

Gower, J. C. 1966. Some distance properties of latent root and vector methods in multivariate analysis. Biometrika, 53: 315–328.

Hansen, A. & Sunding, P. 1985. Flora of Macaronesia. Checklist of vascular plants. 3rd ed. Sommerfeltia, Oslo.

Humphries, C. J. 1979. Endemism and evolution in Macaronesia. In: Bramwell, D. (ed.), Plants and islands, pp. 171–179 Wiley, London.

Kämmer, F. 1974. Klima und Vegetation auf Tenerife, besonders im Hinblick auf den Nebelniederschlag. Scripta Geobotanica. Verlag Erich Goltze KG, Göttingen.

Lausi, D. & Nimis, P. L. 1985. Quantitative phytogeography of the Yukon Territory (NW Canada) on chorological phytosociological basis. Vegetatio 59: 9–20.

Lobin, W. 1982. Untersuchung über Flora, Vegetation und biogeographische Beziehungen der Kapverdischen Inseln. Cour. Forsch. Inst. Frankfurt.

MacArthur, R. M. & Wilson, E. O. 1967. The theory of islands biogeography. Princeton Univ. Press., Princeton.

Quézel, P. 1978. Analysis of the flora of Mediterranean and Saharan Africa. Ann. Missouri Bot. Gard., 65: 479–534.

Rohlf, F. J. 1963. Classification of the Aedes by numerical taxonomic methods. Ann. Entomol. Soc. Amer., 56: 798–804.

Santos, A. 1983. Vegetación de la región Macaronésica. Comunicación al II Congreso pro Flora Macaronésica, Funchal.

Sokal, R. R. & Michener, C. D. 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull. 38: 1409–1438.

Sunding, P. 1979. Origins of the Macaronesian Flora. In: Bramwell, D. (ed.), Plants and islands, pp. 13–40, Wiley, London.

Walter, H. & Lieth, H. 1967. Climate diagram world atlas. Fischer, Jena.