Species composition and within archipelago co-occurrence patterns in the Canary Islands

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The distribution of trees and shrubs, ferns, land birds, beetles, and butterflies on the Canary Islands were analysed according to the null hypothesis approach. Deviations from the expected number of species were found in the species groups trees and shrubs and Tenebrionid beetles. This was interpreted as the result of deterministic processes influencing the colonisation of the archipelago. In an other analysis the relationship between species similarity and geographical distance between the islands was investigated. It showed that species similarity between the island decreased with distance. The decrease was steepest for Tenebrionid beetles and trees and shrubs so it was concluded that their dispersal ability was lower than in the other species groups.

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Introduction

One problem when interpreting geographic distribution of species as evidence for interspecific interactions, as in the theory of assembly rules in species communities (Diamond 1975), is that a null hypothesis, that species are independently distributed, should first be tested. When the idea of the null hypotheses for species distribution was introduced it received a fair amount of attention in the literature on island biogeography and ecology (Diamond and Gilpin 1982, Connor and Simberloff 1983, Harvey et al. 1983). The discussion has centred on the suitability of introducing such a hypothesis in the calculation of random distribution models for islands (Connor and Simberloff 1979, Diamond and Gilpin 1982), particularly with regard to some innate parameters found in archipelagos such as their species-number/area relationships or the species occurrence distributions (number of islands where each species is present).

The species in an archipelago could be considered to belong to one species pool. If the species have equal probabilities for dispersal and persistence then they are equiprobable in this respect. Connor and Simberloff (1978, 1983) have argued that a non-equiprobable species pool is a more realistic assumption, as it is likely that the species in the pool differ in their dispersal or persistence abilities. The different dispersal and persistence abilities for species in the pool is difficult to estimate. It could, however, be assumed that a species actual occurrence on the islands reflects its dispersal and persistence ability. Thus, a species present on a greater number of islands could be assumed to have higher dispersal and better persistence ability than another present on fewer islands. To calculate the expected number of species on an island for a non-equiprobable distribution a method has been developed by Adsersen (1988).

The aim of the present work is to study whether the distribution pattern within different taxonomic groups in an archipelago is random or deterministic. We have chosen five well known taxonomic groups on the Canary Islands assumed to differ in long-distance dispersal abilities; trees and shrubs (Phanerophyta, sensu Raunkiaer 1934), ferns, land birds, Tenebrionid beetles, and diurnal butterflies. We first compared the observed
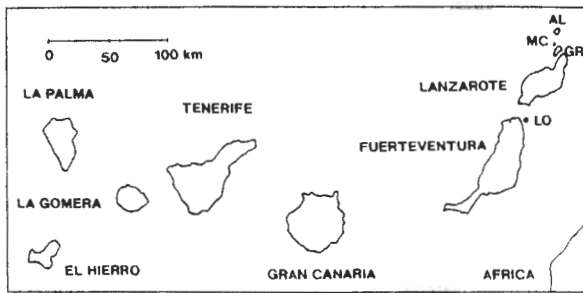

Fig. 1. The Canary Islands. Al = Alegranza, MC = Montaña Clara, GR = La Graciosa and LO = Lobos.

number of species in each group on the islands with the expected according to the ideas of Connor and Simberloff (1978, 1979, 1983) and Adsersen (1988) using a χ^2-test. It was assumed that if the null hypothesis was rejected then deterministic factors were responsible for the distribution pattern. These factors could be either geographical (e.g. water-gaps, wind direction, availability of suitable habitats) and/or ecological (e.g. dispersal or persistence ability, competition, predation, or speciation processes). If the null hypothesis was not rejected then stochastic events would be responsible for the distribution.

In a following analysis we assessed the importance of between-island distance for the distribution of the species. As suggested by Terborgh (1973) it was assumed that if geographic distance and species similarity between the islands are negatively related then a nonrandom structure in the distribution of the species group in the archipelago exists.

Study area

The Canary Islands (Fig. 1) are located in the E part of the Atlantic Ocean (28°N, 16°W), 104 km from Cape Juby the nearest point at the Saharian coast. The archipelago is formed by seven islands, Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro and 4 islets close to Lanzarote and Fuerteventura. The total area of the archipelago is c. 7500 km² and the highest point is 3718 m a.s.l.

Although some earlier authors (e.g. Schmincke 1976) considered the eastern-most islands of the archipelago (Lanzarote, Fuerteventura and the islets) continental, nowadays the whole archipelago is regarded as oceanic (Carracedo 1978). The islands are all of volcanic origin. The oldest rocks recorded were found in Fuerteventura (> 20 million years) and the youngest were formed in the latest volcanic eruption at Teneguía in 1971 on La Palma.

Most of the islands are well separated from each other, with water depths between them that could exceed 3000 m. Lanzarote, Fuerteventura and the islets are, on the other hand, separated only by shallow waters (< 200 m), probably they formed one large island earlier in geological time. The minimum water depth between the archipelago and the African mainland is c. 1500 m, so there has been no land connection.

Materials and methods

The selection of appropriate data sources was a compromise between the suitability and quality of species list available. Within vascular plants (a well-studied group in the Canary Islands) trees and shrubs were selected (check-list by Lems (1960)). The species in this group are generally regarded as good persistors, as indicated

Table I. Number of indigenous species in the investigated taxonomic groups in the Canary Islands.

Island	Area km²	Number of indigenous species				
		Tress, shrubs no.	Ferns no.	Landbirds no.	Beetles no.	Butterflies no.
Lanzarote	796	41	12	32	34	9
Fuerteventura	1725	51	16	33	48	12
Gran Canaria	1532	140	49	45	47	19
Tenerife	2058	169	56	49	47	24
La Gomera	378	110	41	37	24	22
La Palma	729	117	43	36	11	21
El Hierro	278	79	31	30	15	14
Canary Islands	7542	272	59	56	116	26
Endemism (%)						
Insular (1 island)		34.2	3.4	1.8	48.0	0
Archipelago (>1 island)		42.7	5.1	12.5	32.0	26.9
Non-endemic species		23.1	91.5	85.7	20.0	73.1

32

Table 2a. Number of land-birds on the Canary Islands. The diagonal shows the number of species found on each island. The lower triangle shows the observed number of species shared by the island pair. The upper triangle shows the expected number of shared species and in brackets the χ^2-contribution for each island pair.

	Lanzarote	Fuerteventura	Gran Canaria	Tenerife	La Gomera	La Palma	El Hierro
Lanzarote	32	(4.68) 21.07	(0.10) 28.73	(0.35) 31.29	(0.29) 23.62	(0.17) 22.98	(0.07) 19.15
Fuerteventura	31	33	(0.72) 29.63	(1.21) 32.26	(0.46) 24.36	(0.58) 23.70	(0.38) 19.75
Gran Canaria	27	25	45	(0.00) 43.99	(0.00) 33.22	(0.17) 32.32	(0.16) 26.94
Tenerife	28	26	44	49	(0.00) 36.17	(0.00) 35.20	(0.02) 29.33
La Gomera	21	21	33	36	37	(1.55) 26.58	(2.78) 22.15
La Palma	21	20	30	35	33	36	(2.56) 21.55
El Hierro	18	17	29	30	30	29	30

Table 2b. Geographical distance (km), between the islands in the Canary archipelago, upper triangle. Floristic/faunistic similarity (Kulczynski index), lower triangle, of land-bird species on each island.

	Lanzarote	Fuerteventura	Gran Canaria	Tenerife	La Gomera	La Palma	El Hierro
Lanzarote	–	11	167	221	324	378	410
Fuerteventura	0.95	–	81	167	252	324	333
Gran Canaria	0.72	0.66	–	58	126	198	203
Tenerife	0.72	0.66	0.94	–	30	86	112
La Gomera	0.61	0.60	0.81	0.85	–	56	63
La Palma	0.62	0.58	0.76	0.84	0.90	–	68
El Hierro	0.58	0.54	0.81	0.81	0.90	0.89	–

by their long life-span. Ferns are considered to have good long-distance dispersal abilities (check-list by Hansen and Sunding (1985)).

The Canarian fauna is less known. However, Tenebrionid beetles (commonly wingless) were selected as an example of a species group with limited long-distance dispersal ability. Land birds and diurnal butterflies (*Rophalocera*) were chosen as having good dispersal abilities. The sources used were Oromí (1982), Bacallado and Domínguez (1984) and Báez (1984) respectively. The collected information was summarised and the proportion of endemisms was calculated (Table 1).

The intraspecific level was avoided in an attempt to minimise the influence of geographic speciation on the analysis (Connor and Simberloff 1979), especially as the subspecies are largely endemic for each island in the archipelago.

For each taxonomic group a matrix was constructed. The number of species recorded on each island were written in the diagonal. The lower triangle contained the observed number of species shared by the island pair. Total number of island pairs (IP) was 21, IP = n(n-1)/2 (n = number of islands = 7). The upper triangle contained the expected score for shared species.

The expected number of shared species were calculated using the approach by Adsersen (1988) for a non-equiprobable species pool. It assumes that the number of species on each island, the number of islands on which the species occurs and the total number of coincidences are characteristic for the archipelago. Thus:

$$C_{ij} = n_i n_j \, J / \Sigma \, n_i n_j.$$

C_{ij} is the number of expected coincidences between island i and island j; n_i and n_j are the number of species in island i and j respectively. J is the total number of observed coincidence between all pairs of islands. The calculation is only performed when $i > j$.

The χ^2-test (Siegel 1956) was used to evaluate the significance (df = IP-2, $p < 0.05$) of the differences between observed and expected data. However, for the beetles four of the expected values were < 5 so two island pairs were grouped together to allow the test.

In the second analysis floristic or faunistic similarity was calculated for each pair of islands. To calculate the similarity Kulczynski's index $((C/A) + (C/B))/2$ was used where A and B are the number of species on each island and C the number of shared species (Kulzcynski 1927, Hubalek 1982). It was used to avoid low similarity values when comparing islands with large differences in

Table 3. Number of island pairs (IP), number of species (N), total number of species coincidences (J), χ^2-values, significance (p).

Taxonomic group	IP	N	J	χ^2	p	Source
Trees and shrubs	21	272	1134	69.99	<0.01	Lems (1960)
Ferns	21	75	456	33.23	n.s.	Hansen and Sunding (1985)
Land birds	21	56	584	16.25	n.s.	Bacallado and Domiguez (1984)
Beetles	21	116	218	75.59	<0.01	Oromí (1982)
Butterflies	21	26	263	7.35	n.s.	Bàez (1984)

species number. The obtained similarity scores were used in a regression analysis on similarity versus between-island distance. The distance between the islands was measured as the distance between the nearest points.

A matrix was constructed containing the geographic distances between islands pairs and the associated similarity index. As an example, the matrices for land birds are given in Tables 2a and b. Matrices for the other investigated groups are available on request.

Results

The relative importance of endemism in the studied taxonomic groups was assessed (Table 1). It showed that both beetles and trees and shrubs have high proportions (> 30%) of local or insular endemisms whereas the other groups have values < 5%. Butterflies, trees and shrubs and beetles, have a high proportion of Canarian endemisms (present on 2 or more islands). The non-endemic indigenous element is important in ferns, land birds and butterflies (> 70%).

Only for two of the investigated species groups, trees and shrubs and Tenebrionid beetles, the observed species numbers were significantly different from the expected i.e. the null hypothesis was rejected. Thus, for ferns, land birds and diurnal butterflies the null hypothesis was not rejected (Table 3).

All the investigated species groups, except land birds, showed a significantly higher number of occurrences than expected on the eastern-most islands: Lanzarote and Fuerteventura (Table 2a).

The analysis of between island geographic distance and taxonomic similarity (Fig. 2) showed that the similarity of the species composition was significantly related to the distance between the islands. Moreover, it showed that similarity decreased with distance with a similar slope for all the groups except ferns. However, the intercept varied between the groups.
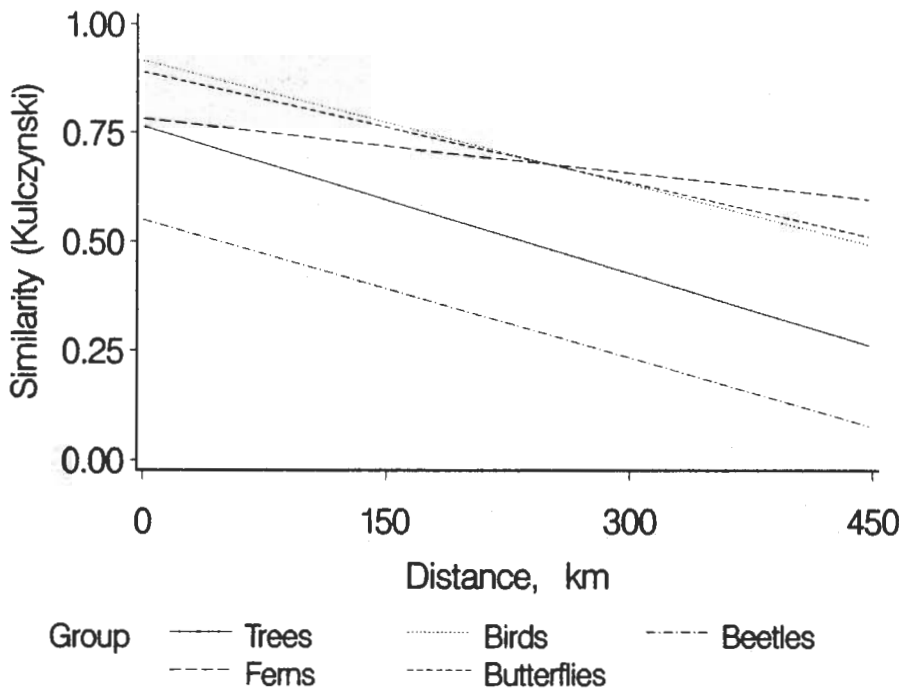

Fig. 2. Linear regression of similarity index (Kulczynski) vs geographical distance between the Canary Islands for land birds: (z = -0.09 100 km^{-1}, y = 0.91, r^2 = 0.77, p < 0.001), butterflies (z = -0.08 100 km^{-1}, y = 0.89, r^2 = 0.53, p < 0.01), trees and shrubs (z = -0.11 100 km^{-1}, y = 0.76, r^2 = 0.87, p < 0.001), ferns (z = -0.04 100 km^{-1}, y = 0.78, r^2 = 0.34, p < 0.01) and beetles (z = -0.11 100 km^{-1}, y = 0.55, r^2 = 0.59, p < 0.001).

Discussion

Some authors (Grant and Abbott 1980, Diamond and Gilpin 1982, Wright and Biehl 1982, Schoener 1982, Gilpin and Diamond 1984) regard competition as the major cause of species distribution and co-occurrence patterns in archipelagos. They claim that null hypothesis testing, using species-area and species occurrence data from investigated archipelagos, will be difficult to use as it may lead to erroneous conclusions. We suggest, however, that null hypothesis testing is a sound technique to identify patterns in species distributions associated with e.g. dispersal abilities in an archipelago.

The null hypothesis was not rejected for ferns. Adsersen (1988) has found the same pattern for pteridophytes on the Galápagos islands. Neither was it rejected for land birds or butterflies thus, it was concluded that these species groups show a random distribution over the archipelago. On the other hand, the null hypothesis was rejected for Tenebrionid beetles and trees and shrubs. The distribution and co-occurrence of these species groups in the archipelago was thus concluded to be deterministic. Both these latter species groups are also regarded as poor long-distance dispersers. A comparison of tree and shrub versus fern data suggests that there could be a correlation between long-distance dispersal ability and the difference between observed and expected co-occurrences.

Except for land birds, Lanzarote and Fuerteventura share more species than should be expected. This is probably due to the close position of these islands to the continent or to the fact that both islands formed one large unit in earlier geological time.

The assumed long-distance dispersal ability of the studied groups was inversely related with the proportion of insular endemisms (Table 1). Thus, species co-occurrence patterns shown by species with poor dispersal ability are characterised by a large number of insular endemisms species not shared by other islands; a result of the speciation processes. According to Williamson (1981) speciation is higher for these groups than immigration. Species with good long-distance dispersal ability are represented by a large number of non-endemic species, thus showing faster immigration than speciation. This may argue against the use of groups with well-developed endemic elements for testing of the null hypothesis for species distribution.

The relationship between geographical distance and species occurrence similarities were calculated to detect the existence of a distribution structure. Significant relations were expected for groups showing a deterministic component in their distribution pattern, i.e. trees and shrubs and beetles. However, this structure was also present in groups distributed randomly (ferns, land birds and butterflies), as can be inferred by the coefficient of determination (r^2) at the $p < 0.01$ level (Fig. 2).

If the validity of the null hypothesis test is accepted and consequently the random distribution of ferns, land birds and butterflies concluded, then the structure found in the regression analysis must be explained in terms of size and location of the islands within the archipelago. An explanation could be that in the Canaries small islands are found in the outer parts, while the largest are found in the centre and larger islands usually have more species than smaller (Fig. 1).

A random distribution of species will exist only if the larger islands have more species than the smaller. In this case, larger islands will share more species with each other (high similarities) than with the smaller (low similarities). Geographical distances between the large islands are short, between small and large islands intermediate and between small islands at each extreme of the archipelago long. In an indirect way, this supports the "Random placement theory" (Arrhenius 1921, MacGuinness 1984) where large areas (islands) due to randomness have higher species number than smaller.

If the structure found in the regression analysis is due to deterministic processes, it could not explain the distribution of ferns, land birds and butterflies. Thus, the validity of the null hypothesis model used to test the coincidence patterns would be doubted.

Terborgh (1973) argues that the slope of the line relating geographical distance between islands with the species co-occurrence similarity represent the taxonomic turnover i.e. floristic/faunistic changes between island biotas (Fig. 2). The slope may be expressed as a similarity decrease 100 km^{-1}. A group showing a flatter slope such as ferns, should be regarded as containing better long-distance dispersers than groups with steeper slopes such as trees and shrubs or beetles.

The intercept includes two different sources of information. Firstly, the stochastic "noise" (for groups showing co-occurrences and distribution patterns due to deterministic processes) related to random differences in their recent histories regarding immigration and extinction. Secondly, it is influenced by inter-island differences in area, habitat diversity or isolation, factors important for the insular endemic element. Beetles had low intercepts which agrees with their high degree of insular endemism (Table 1). Ferns, trees and shrubs and butterflies groups with different levels of endemisms, obtained an intermediate intercept value. Finally, land birds showed a high intercept probably related to the low level of insular endemic elements in the group.

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