

# Geographical determinants of the biological richness in the Macaronesian region

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## Abstract

Several geographical factors determine the biological richness of oceanic islands and archipelagos. To investigate the importance of these factors we used data on flowering plants, ferns, land birds, beetles and butterflies of the native biota of the Macaronesian region (the archipelagos of the Azores, Madeira, the Canaries and Cape Verde). The five taxonomic groups vary in long-distance dispersal ability.

Three different analyses varying in level of approach were carried out: a Macaronesian or between-archipelagos approach, a Canarian or within-archipelago approach and finally a multiple island approach. It shows that at the first level age and isolation are important factors in determining the richness of the groups with low dispersal ability, whereas area and height better predict the richness of taxonomic groups with good long-distance dispersal ability. At the within-archipelago level, area and habitat diversity usually were the most important factors determining the biological richness, although some factors related with features of the nearest neighbouring island also play a role in explaining the richness of taxonomic groups with good dispersal ability. Finally, two sets of islands that varied in area but not in habitat diversity and *vice versa* were selected and analysed to compare the 'area *per se*' and the 'habitat diversity' hypotheses. The results do not support the latter hypothesis.

**Keywords:** Bird; Canaries; Insect; Island age; Species richness; Vascular plant.

**Abbreviations:** ANI = area of nearest neighbouring island; DNI = distance to nearest neighbouring island; HD = habitat diversity; HNI = height of nearest neighbouring island.

## Introduction

A survey of literature dealing with island biogeography and ecology (e.g. MacArthur & Wilson 1967; Carlquist 1974; Gorman 1979; Williamson 1981; Mueller-Dombois et al. 1981; Menard 1986; Whittaker 1998) led to the idea that different geographical determinants can be claimed to play roles in controlling the biological richness of oceanic islands or archipelagos. Among the suggested geographical determinants, we have chosen five major features of islands: (1) Latitude; (2) Area; (3) Height a.s.l.; (4) Degree of isolation and (5) Geological age.

Island latitude influences the biological richness as it controls the macroclimatic features of the island or islands group, basically in terms of annual temperature range and water availability. Thus, in the same way as boreal or temperate forests are less rich than tropical ones, tropical islands (e.g. Hawai'i) are expected to have biotas richer than temperate (e.g. Azores) or boreal (e.g. Iceland) islands (Mueller-Dombois 1992). Furthermore, the geographical location of an island will determine, due to the general wind and marine current regimes of the zone, the origin of the bulk of its biota and the pace of species arrival to the island.

The role of the island area in controlling its species number has been stressed by several authors (Arrhenius 1921; Gleason 1922; Preston 1962). The importance of island area is included in two of the three main theories in island biogeography:

- The 'Random placement' or 'Null hypothesis theory' (Connor & McCoy 1979; Coleman et al. 1982) points out the importance of island area in relation to the likelihood of colonization events of species from the continental species pool.
- The 'Equilibrium theory' (MacArthur & Wilson 1963, 1967) highlights the role of area for the size of the island populations involved and thus, for the likelihood of extinction events.

Both theories, although arguing from different points of views, thus agree that richer biotas are found on larger islands when compared to smaller ones.

The direct relation between height of the island and the number of different habitats that it can have is a major geographical factor explaining the richness of insular biotas in the 'Habitat diversity hypothesis' (Williams 1964). The higher the island, the more zonal ecosystems (with an altitudinal distribution) exist on the island and thus, the larger are the differences in the environmental conditions to be exploited. Height repeats on the island the latitudinal climatic variation, enabling the development, although with some differences, of the latitudinal zonation of terrestrial vegetation. Moreover, altitude, together with wind regime causes the island to develop well differentiated slope types (windward and leeward) and can thus increase the habitat diversity and species number.

Isolation, expressed as the water gap existing between the island and the nearest continent, is also claimed to be a major determinant of the biological richness of an island by the 'Equilibrium theory'. The isolation will determine which species can reach an island, a large fraction of the continental species pool when the distance is short, or only species with good long distance dispersal ability when it is large. Some classic works (e.g. Firth & Davidson 1945; Carlquist 1965) state that there is a decrease in the number of species in a given taxonomic group in relation to the islands' distance to the continent. However, isolation may also increase the biological richness of distant islands, as the non-existence of genetic interchanges between the continental and island populations could give rise to speciation processes that increase the island's biota.

Finally, geological age of an island has to be an important factor explaining its biological richness. Although this is not claimed in the classical theories dealing with island biogeography. First, the likelihood of a species to arrive at an island is related to the island's age as it may be expected that a larger number of events have occurred on older islands than on younger. Second, younger islands usually acquire their biota from older ones. On the other hand and similar to the effect of isolation, the age of an island plays a role in the speciation processes, because the older the island the further has the speciation process on the island proceeded. Finally, the erosion processes also influence the biota because they increase the actual area (not the projected area) of an island by creating new azonal habitats (such as ravines or cliffs) which tend to increase the richness of the biota.

Other geographical determinants, such as distance to the nearest island, area of the nearest island, height of the nearest island, distance to the nearest larger island, distance to the nearest older island, and so on, have been used in different biogeographical analyses (Johnson & Simberloff 1974; Connor & Simberloff 1978; Nilsson et al. 1988). However, these factors are combinations of the main ones and may have a significance only for a single archipelago.

The existence of different island biogeography theo-

ries may be explained by an indiscriminate use of data to support them. Data have been obtained from real islands or archipelagos with different latitudinal location, origin (oceanic or continental), size, age or isolation, sometimes even from 'pseudo-islands' (as varied as mountain tops, habitat islands, ponds and inflorescences). Such data have almost always involved different taxonomic groups and levels. Some authors (e.g. Connor & McCoy 1979) who have tried to recompile available data to analyse them in the light of the different theories usually finished without clear conclusions.

The aim of our work has been to find more reliable data and to investigate the relationships of geographical and biological factors within oceanic archipelagos. The archipelagos within the Macaronesian region have a well-known flora and fauna and thus provide a good opportunity to compare how the selected geographic determinants influence their species number. In particular we have studied the number of species in different taxonomic groups varying in dispersal ability in relation to a wide range of latitude, area, height, isolation and age of the islands (cf. Table 1).

## Study area

The Macaronesian region (Fig. 1 and Table 1) is composed of four Atlantic archipelagos; The Azores, Madeira, The Canaries and Cape Verde, located off the European and African mainlands. The archipelagos embrace the latitudes between 15° N (Cape Verde) and 40° N (Azores). Their degree of isolation, i.e. the distance from the nearest continent, varies from 95 km between the Canaries and the Saharan coast to 1 450 km between the Azores and the Portuguese coast. The Canaries form the largest archipelago (7480 km<sup>2</sup>) with the highest peak (3718 m on Tenerife), but the Azores (2351 m on Pico) and Cape Verde (2835 m on Fogo) are quite high too.

Table 1. Geographical (number of islands, latitude, area, height, isolation and age) and biological (number of native vascular plant species, land birds and *Tenebrionidae* beetles) features of the Macaronesian archipelagos Azores (Az), Madeira (Ma), Canary Islands (Ca) and Cape Verde (CV).

	Az	Ma	Ca	CV
No. of islands (> 1 km <sup>2</sup> )	9	3	11	10
Latitude (°N)	37-40	32-33	28-29	15-17
Area (km <sup>2</sup> )	2388	815	7447	3580
Height (m a.s.l.)	2351	1846	3718	2835
Isolation (km)	1450	540	95	500
Age (million yr)	8.1	13.5	20.5	10.3
No. of vascular plants	300	750	1260	560
No. of land birds	27	27	58	32
No. of beetles	7	27	113	28



Fig. 1. Location of the Macaronesian region.

## The volcanic origin of the archipelagos

The Macaronesian archipelagos share their volcanic origin. All the islands can be considered as oceanic, that is, they have emerged after successive submarine eruptions of basic magma (mainly basalts), through different ocean crust fractures. Some islands, notably Lanzarote and Fuerteventura (Canaries), are located at the transition zone between the continental and oceanic crusts, because of their proximity to the African continent; here the ascending magma carried also fragments of sedimentary rocks belonging to the African continental margin.

Anyhow, the origin of all the archipelagos can be understood as a consequence of the North Atlantic internal geodynamics, with magma emitted mainly through the Mid-Atlantic Ridge, but also through fracture zones and transforming faults, since its opening almost 180 million yr ago. Recent oceanographic research of the Atlantic floors has revealed that the ocean floor is moving away from the central ridge in both directions at a speed of 1-2 cm/yr. This means that the westernmost islands of the Azores, Flores and Corvo, actually located on the American tectonic plate, are being separated from the rest of the archipelago.

With the exception of the Azores, the archipelagos are included in the African tectonic plate, which implies that they have a weaker seismic and volcanic activity. On the other hand, the Azores, located at the NW edge of the African plate and at both sides of the Mid Atlantic Ridge show a high seismic and volcanic activity – during recent years, some very destructive earthquakes have occurred here (García-Talavera 1999).

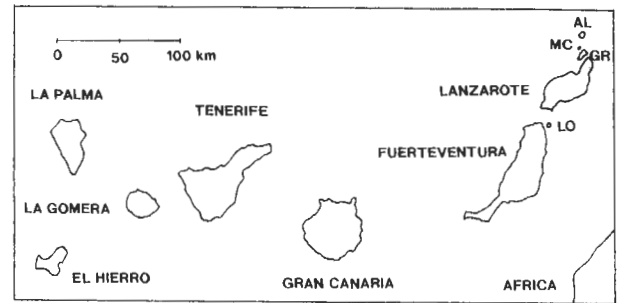


Fig. 2. Location of the Canary Islands. AL = Alegranza, GR = La Graciosa, MC = Montaña Clara, LO = Lobos.

The ages of the archipelagos vary from ca. 20 million yr for the Canaries (Coello et al. 1992) to ca. 8 million yr for the Azores (Ridley et al. 1974). The Cape Verde islands, traditionally considered as the oldest archipelago of the region (due to findings of rocks dated more than 100 million yr old) are probably younger than the Canaries, nowadays considered to be between 8 and 10 million yr old (Bernard-Griffiths et al. 1975). Historic volcanism (from the European colonization onwards, i.e. the last 500 yr) has been present in the Azores (Sao Miguel, Terceira, Sao Jorge, Pico y Faial), Canaries (Lanzarote, Tenerife and La Palma) and Cape Verde (Fogo) (Báez & Sánchez-Pinto 1983). This century eruptions include Capelinhos (1957) on Faial, Chinyero (1909) on Tenerife, San Juan (1949) and Teneguía (1971) on La Palma as well as Pico do Fogo (1951, 1995) on Fogo.

Macaronesia was first considered a biogeographical regional unit due to the many common geographical and biological characteristics. This has been accepted for more than a century (Sunding 1979). However, some authors have recently highlighted the floristic heterogeneity within the region (Lobin 1982; Nicolás et al. 1989) questioning the inclusion of Cape Verde and Azores in the same biogeographical region.

The Canary Islands (Fig. 2) are located in the eastern part of the North Atlantic Ocean (28°N, 16°W), 95 km from Punta Stafford on the Saharian coast. The archipelago includes seven main islands – Tenerife, Fuerteventura, Gran Canaria, Lanzarote, La Palma, La Gomera and El Hierro – and four islets – La Graciosa, Alegranza, Lobos and Montaña Clara. Although some earlier authors (see Schmincke 1976) considered the easternmost islands of the Canarian archipelago – Lanzarote, Fuerteventura and the islets – as continental, nowadays the whole archipelago is regarded as oceanic (Banda et al. 1981). The central and western islands are separated from each other by ca. 3000 m deep water, whereas the eastern ones are separated by relatively shallow waters (< 200 m); earlier they have formed one single island, the Eastern Canarian Ridge (Coello et al. 1992). No connection is known be-

tween the archipelago and the African mainland, the water depth is about 1000 m.

Within the Macaronesian region, the Canary islands were selected for an archipelago-level analysis due to the high variability shown by the geographical determinants between the islands: (1) areas differing between 2034 km<sup>2</sup> for Tenerife (the largest island of Macaronesia) to 1.3 km<sup>2</sup> for Montaña Clara; (2) heights varying from 3718 m (Teide Peak on Tenerife, the highest point in the Atlantic and only surpassed by the Hawaiian peaks on the global scale) and 122 m for Lobos; (3) isolations ranging from 95 km for Fuerteventura to 424 km for La Palma; (4) and ages varying from ca. 20 million yr for the Eastern Canarian Ridge (Lanzarote and Fuerteventura) to several thousands for the islets.

Furthermore, the Canaries have by far the richest biota of the region, a biota closely related to the Mediterranean and Saharan ones. However, certain spectacular affinities to South or East African and South American plant genera (Sunding 1979) or Indo-Burman insect genera (Báez 1984) are found. The proportion of endemic species varies between the different taxonomic groups, from 100% for reptiles to ca. 50% for vascular plants to low or non-existent for groups with long-distance dispersal ability such as land birds or winged insects.

The first data on island sizes and number of species for the Canary Islands were published by von Buch (1825). However, it was not until the beginning of the 1960s that Hemmingsen (1963) plotted the first species-area curve for the archipelago. He included also Madeira and used data collected by Volsoe (1955) on breeding birds. Simberloff (1970) used the same data to calculate the taxonomic diversity of the Canary Islands' avifauna. Connor & McCoy (1979) used data by Lems (1960) on vascular plants and Simberloff's data (1970) on avifauna to calculate correlation coefficients, slopes and intercepts for the species-area relationship using different regression models. In recent years, different works dealing with general biogeographical aspects concerning the Canary Islands have appeared (Báez 1987; de Nicolás et al. 1989; Becker 1992; Fernández-Palacios & Andersson 1993).

## Methods

To analyse the geographical determinants that control the biological richness we used three different levels of scale:

1. The first level represents the 'Macaronesian approach' where we analysed the archipelagos as single entities and paid special attention to the consequences of variation in latitude and isolation. Latitudinal variation has little importance within an archipelago when the difference between the northernmost and the southernmost islands is only a few degrees. This is the case for the Macaronesian archipelagos, because they are also mainly longitudinally

distributed. On the other hand, isolation may be ignored within an archipelago, as the distances between islands within an archipelago usually are shorter than the distance to the mainland. However, the possible role of the water-gap between islands is analysed at the archipelago level.

2. The second level is the 'archipelago approach', which was followed for data from the Canaries. At this level we analysed the influence of area, height and age and also other factors such as habitat diversity, number of zonal ecosystems found on the island (*sensu* Humphries 1979), area of the nearest island (ANI), height of the nearest island (HNI) and distance to the nearest island (DNI) (Table 2).

We also carried out three different correlation analyses. First, the geographical determinants were subjected to a correlation analysis to detect covariation within the data set. Secondly, the richness of the different taxa were subjected to the same approach. Finally, single regressions of biological richness (dependent variables) to geographical factors (independent variables) were calculated for the whole data set using four different regression models: linear, logarithmic, exponential and power.

3. A multiple comparison between single islands belonging to the same or different archipelagos was also carried out. The aim was to analyse the influence of some factors on islands similar to one another. It has been suggested (Abbott 1980; van der Werff 1983) that islands within an archipelago with the same number of habitats but different size, or *vice versa*, could be used to obtain information on the 'Area *per se*' versus 'Habitat diversity' controversy (Simberloff 1974; Abbott 1980).

First we compared islands within an archipelago – the eastern Canarian Islands and islets: Montaña Clara (MC), Lobos, Alegranza, La Graciosa, Lanzarote and Fuerteventura (FV). These islands vary in area but not in habitat diversity, latitude and isolation. They have only one habitat (subdesert scrub) but their areas range from 1 km<sup>2</sup> (MC) to 1725 km<sup>2</sup> (FV). A second comparison was carried out on islands with similar areas but varying in height and thus in habitat diversity: Lanzarote (796 km<sup>2</sup>), Madeira (728 km<sup>2</sup>) and La Palma (729 km<sup>2</sup>), with habitats: one, three and five respectively.

For the selection of taxonomic groups we used two criteria: (1) the data should be reliable and update and (2) the taxonomic groups should vary in long-distance dispersal ability. Five groups were found to fulfil these requirements and were thus selected: ferns, flowering plants, land birds, beetles (*Tenebrionidae*) and butterflies.

Hansen & Sunding's (1985) checklist for both ferns and flowering plants of the Macaronesian flora was used for the Macaronesian analysis. The archipelago (Canarian) analyses were instead carried out using the more recent work by Kunkel (1993), that also includes data for the islets. The data on flowering plants were also combined to allow an analysis on as many islands as possible throughout Macaronesia; in total data for 34 islands were available.

Table 2. Geographical and biological features of the Canary Islands and Madeira. HD = habitat diversity; ANI = area of nearest neighbouring island; HNI = height of nearest neighbouring island; DNI = distance to nearest neighbouring island. Species richness, i.e. the number of species is indicated for ferns (fern), flowering plants (flow), land birds (bird), beetles (beet) and butterflies (butt); - = no data available.

Island	area (km <sup>2</sup> )	height (m)	isolation (km)	age (10 <sup>6</sup> yr)	HD	ANI (km <sup>2</sup> )	HNI (m a.s.l.)	DNI (km)	fern	flow	bird	beet	butt
Tenerife	2034	3,718	292	11.9	6	370	1,487	30	41	804	49	47	24
Fuerteventura	1655	807	95	20.5	1	4	122	2	14	406	33	48	12
Gran Canaria	1560	1950	200	14.5	4	2034	3718	58	40	745	45	47	19
Lanzarote	807	671	132	15.5	1	27	266	1	12	382	32	34	9
La Palma	708	2423	424	1.5	5	370	1487	56	39	501	36	11	21
La Gomera	370	1487	340	12.0	3	2034	3718	30	33	518	37	24	22
El Hierro	269	1501	388	0.8	4	370	1487	63	24	402	30	15	14
La Graciosa	27.5	266	153	-	1	807	671	1	0	116	20	-	-
Alegranza	10.2	289	167	-	1	1.3	256	7	0	81	17	11	-
Lobos	4.4	122	122	-	1	1655	807	2	1	113	15	9	-
Montaña Clara	1.3	256	162	-	1	27	266	2	0	62	10	3	-
Madeira	728	1846	540	5.0	3	69	520	40	73	711	27	37	15

The Canarian checklist by Bacallado & Domínguez (1984) on breeding land birds was completed for the Azores and Cape Verde islands with Le Grand's works (1984, 1986) and for Madeira with Jones et al. (1987). Data of the Canarian islets, not included in the checklist were obtained from Martín (pers. comm.). We excluded sea birds from the analyses. The works by Oromí (1982a, b) provided data on Canarian and Macaronesian beetles; these data were completed for the Canarian islets (Oromí pers. comm.). Finally, the data from Báez (1984) on butterflies were used only in the Canarian analysis.

In general, the proportion of endemic species are low for groups having long-distance dispersal ability (ferns, land birds and butterflies), and relatively high for plants: ca. 50% for the Canaries, beetles: ca. 50% for Madeira and Cape Verde and up to 80% for the Canaries. Finally, it was assumed that the species lists include an error source. However, the level of knowledge on the analysed taxa in Macaronesia is great enough that one need not to consider it likely that the species number on each island is better correlated with the number of scientific expeditions than to any geographical variable, as seems to occur for instance in the Galápagos (Connor & Simberloff 1978).

## Results and Discussion

At the Macaronesian level, the only significant correlation identified between the geographical determinants was that between area and height of the islands (Table 3a). Table 4 shows the results of the Macaronesian approach, where latitude, area, height, isolation and age of the four archipelagos were correlated with number of vascular plants, land-birds and beetle species. A further analysis of the 34 islands was carried out, but only for vascular plants.

At this level, the age of the archipelago is a significant predictor for vascular plants and beetles, but not for land-birds. Moreover, isolation was also a significant determi-

nant for beetles, whereas area only was found to be a good predictor for land-birds richness. However, the analysis of the 34 islands showed that area and height, but not age, were significant predictors of their richness. Therefore, number of islands and latitude were the only factors not found to be significant for any taxonomic group at the Macaronesian level.

As expected, the age of the archipelagos is correlated with groups with large proportions of endemic species as time is a major requirement for speciation events. On the other hand, age was not a significant factor for land-bird richness, a group with a low endemic rate in Macaronesia and generally considered as good dispersors. Isolation could only explain beetles richness (high on the near-to-continent Canaries and Madeira and low on the far-to-continent Cape Verde and Azores); this is reasonable if it is considered that this is the group with the lowest long-dispersal ability amongst the studied groups. We showed in an earlier study (Fernández-Palacios & Andersson 1993) that for the Canaries taxonomic groups which are assumed to have good long-distance dispersal abilities as land-birds show a stochastic colonization pattern in the archipelago, whereas a deterministic pattern was found in groups with poor ability for long-distance dispersal.

The analysis of the 34 islands, performed exclusively for vascular plants, highlights the importance of both area and height of the island. Nevertheless, as seen above, both factors are correlated and it is not possible to distinguish which of them is ultimately responsible. Thus, specific analyses were performed, where variation in island area was not connected with variation in island height or *vice versa*.

Finally, the fact that latitude is not found to be significant in any taxonomic group, may be attributed either to its lack of explaining biological richness on islands, or to the latitudinal variation within Macaronesia (25°) as not being large enough to control the pattern of variation in biological richness.

Table 3a. Matrix of linear correlations between the independent variables throughout Macaronesia. b. Matrix of linear correlations between the independent variables in the Canary islands. HD = habitat diversity; ANI = area of nearest neighbouring island; HNI = height of nearest neighbouring island; DNI = distance to nearest neighbouring island. Only significant values are shown; n.s. = non-significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ .

a.					b.							
Area	n.s.				Height	0.71*						
Height	n.s.	0.99**			Isolation	n.s.	0.67*					
Isolation	n.s.	n.s.	n.s.		Age	n.s.	n.s.	-0.91**				
Age	n.s.	n.s.	n.s.	n.s.	HD	n.s.	0.96**	0.80**	n.s.			
	Latitude	Area	Height	Isolation	ANI	n.s.	n.s.	n.s.	n.s.	n.s.		
					HNI	n.s.	n.s.	n.s.	n.s.	n.s.	0.81**	
					DNI	n.s.	0.68*	0.82**	-0.78*	0.83**	n.s.	0.68*
						Area	Height	Isolation	Age	HD	ANI	HNI

When the multiple correlation analysis of the geographical features in the Canaries was performed (Table 3b), it showed that more than half of the combinations were correlated. Some of the correlations between geographical variables at the archipelago level, could be interpreted as general features for islands and archipelagos, such as Area-Height, Height-HD or ANI-HNI. Other correlations seem to be specific for the archipelago due to its shape. The correlations between DNI-HNI, DNI-HD and Isolation-HD are likely to be an effect of the existence of an eastern group of low islands close to each other and to the African mainland. Finally, the significant correlation found between Age and HD may be attributed to the fact that old islands (as Lanzarote and Fuerteventura) which have been eroded for several millions of years and nowadays are low and flat, in fact display low habitat diversity.

When the correlation between richness of the different taxonomic groups (Table 5) was calculated, we found some interesting points: (1) land-bird richness is correlated with the richness of all the other taxonomic groups; (2) vascular plants richness is a better predictor of fern richness than any of the geographical factors analysed; and (3) butterfly richness is only correlated with land-bird richness. In general, significant correlations were also obtained for a major part of the taxa group combinations.

Table 6 shows the results of the single regressions of

Table 4. Regressions of the main geographical factors versus richness (number of species of vascular plant, land birds and *Tenebrionidae* beetles) on each Macaronesian archipelago, and versus vascular plant richness of 34 islands throughout Macaronesia (sensu Hansen & Sunding 1985)  $n$  = number of archipelagos or islands included in the calculation; model = type of regression model;  $r$  = correlation coefficient. Only significant values are shown: \* =  $p < 0.05$  and \*\* =  $p < 0.01$ .

Taxonomic group	Factor	n	Model	$r$	Significance
Vascular plants	Age	4	lin	-0.95	*
	Area	34	pwr	0.79	**
	Height	34	pwr	0.81	**
Land-birds	Area	4	lin	0.95	*
Beetles	Isolation	4	pwr	-0.97	*
	Age	4	pwr	0.96	*

taxonomic richness vs. geographical features at the within archipelago level. As much as the 50% of all possible combinations are significant descriptors of the richness of any taxonomic group. From them, area has been found to be the best descriptor for the richness of vascular plants, land-birds and beetles. On the other hand, area was not a significant factor for ferns, where DNI was found to be the best predictor, height was a better predictor for richness of butterflies. Moreover, height was the single factor significant for all groups. Furthermore, habitat diversity (correlated with height) was found to be significant for all groups except beetles, whilst age (only significant for beetles) or isolation (only found to be significant for ferns) seems not to play an important role at this level. Finally, it is worth noting that geographical features of the island nearest to the one analysed (such as distance to, and area or height) were only significant for groups with good dispersal ability. The population of the neighbouring islands may thus act as a reservoir safeguarding local extinction.

The results obtained clearly differ from those found by Connor & McCoy (1979), for the seven main Canary Islands. The improvement of the checklists over the last decade and the inclusion of the islets in the analyses are probably the reasons for this discrepancy. Thus, comparisons carried out between taxa without and taxa with data for the islets may lead to unrealistic conclusions. A further problem in the interpretation of the data appears with the taxonomic groups (such as butterflies) where all the species are present on the largest island, Tenerife, and the species number therefore does not reach the number in the species pool asymptotically.

Table 5. Matrix of linear correlations between the richness of the studied taxonomic groups in the Canary Islands. Only significant values are shown; n.s. = non-significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ .

Ferns	0.89**			
Land birds	0.89**	0.62*		
Beetles	0.77**	n.s.	0.75*	
Butterflies	n.s.	n.s.	0.71*	n.s.
	Flowering plants	Ferns	Land birds	Beetles



Table 6. Best significant regression for each taxonomic group of geographical factors vs. species richness in the Canary Islands. HD = habitat diversity; DNI = distance to nearest neighbouring island;  $n$  = number of islands in calculation; model = type of regression model;  $r$  = correlation coefficient. Only significant values are given: \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ .

Taxonomic group	Factor	$n$	Model	$r$	Significance
Vascular plants	Area	12	pwr	0.95	**
	Height	12	log	0.92	**
	HD	12	log	0.82	**
	DNI	12	log	0.72	**
Ferns	DNI	8	pwr	0.82	*
	Isolation	8	pwr	0.81	*
	Height	8	pwr	0.80	*
	HD	8	pwr	0.77	*
Land birds	Area	12	pwr	0.96	**
	Height	12	log	0.88	**
	HD	12	lin	0.77	**
	DNI	12	log	0.60	*
Beetles	Area	11	pwr	0.90	**
	Age	8	pwr	0.81	*
	Height	11	pwr	0.63	*
Butterflies	Height	8	pwr	0.88	**
	HD	8	pwr	0.85	**
	HNI	8	pwr	0.78	*
	ANI	8	pwr	0.76	*
	DNI	8	pwr	0.76	*

Of the regression models, the power model is the better one with about 70% of all significant regressions. However, both the logarithmic (25%) and the linear models (5%) are also represented. Thus, it is difficult to consider only one of them as universal in island biogeography, as also has been pointed out by Connor & McCoy (1979) and Rydin & Borgegård (1988).

The results from the multiple island comparison level are shown in Table 7. It was not possible to compare the influence of a single geographical variable on the insular biological richness. Thus, this analysis was exclusively carried out to throw some light on the classical controversy on the role of area or habitat diversity in explaining the biological richness of a given island.

Results of the first approach, where islands varying in area but not in HD, isolation and latitude were compared (the eastern Canarian Ridge), show an increase in richness in all cases analysed (plants, land birds and beetles) although there was no increase in the number of habitats. Results show that the slopes of the power regression lines,  $z$ -values, for plants (0.27), fit well within the range of values (0.18-0.35) (Diamond & May 1976) expected by the Equilibrium theory (MacArthur & Wilson 1963, 1967) and was confirmed for different taxonomic groups in numerous oceanic archipelagos around the world (Diamond & May 1976; Williamson 1981). However, both land birds (0.16) and beetles (0.34)  $z$ -values stay close to the lower and upper limits respectively, questioning its validity for the Canaries.

Nevertheless, Connor et al. (1983), stated that the

Table 7. a. Power regressions of area vs. species number for the studied taxonomic groups on the Eastern Canarian Islands and islets, varying in area but not in number of habitats;  $n$  = number of islands in the analysis;  $r$  = correlation coefficient and significance level; n.s. = not significant; \* =  $p < 0.01$ ; \*\* =  $p < 0.05$ . b. Linear and power regression models of habitat diversity versus species number for the studied taxonomic groups on the islands of Lanzarote, Madeira and La Palma, varying in number of habitats but not in area.

a.					
Taxonomic group	$n$	$r$	Slope ( $z$ )	Y-intercept	Significance
Flowering plants	6	0.97	0.27	56.11	**
Land birds	6	0.99	0.16	11.01	**
Beetles	5	0.98	0.34	3.95	**
b.					
Taxonomic group	$n$	$r$ -linear	Significance	$r$ -power	Significance
Ferns	3	0.45	n.s.	0.79	n.s.
Flowering plants	3	0.36	n.s.	0.61	n.s.
Land birds	3	0.44	n.s.	0.21	n.s.
Beetles	3	-0.81	n.s.	-0.70	n.s.
Butterflies	3	1.00	**	0.99	*

occurrence of the slopes in the expected range does not necessarily imply the acceptance of the theory. Moreover, a large proportion of power regression lines fitted this range and could sometimes be considered as a statistical artefact (Loehle 1990).

On the other hand, the results of the second approach, where islands vary in HD but not in area and latitude, show an erratic pattern, with trends varying between the different taxonomic groups. With the exception of butterflies, where the increment in habitat diversity is associated with a significant increment of the insular richness (for both the linear and the power model), the rest of the groups do not show an increasing trend, and even the beetles show a decreasing one.

The results of the two multiple island comparisons seem to support both the Area *per se* and the Random placement hypotheses, opposite to what Mueller-Dombois & Fosberg (1998) found for the tropical Pacific islands. The Area *per se* hypothesis explains the higher number of species on larger islands as a result of lower extinction rates, due to larger populations involved, whereas the Random placement theory attributes the higher richness of larger areas to stochastic distributions. However, the Habitat diversity theory where the species richness is largely due to the number of different habitats was not supported by our data.

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