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Environmental determinants of island species numbers in the British Isles

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Abstract

Regression analyses were computed for the prediction of island species numbers in the British Isles, using as independent variables island area, island elevation, the number of soil types, °N latitude, the distance from mainland Britain, the distance from the nearest other island, the number of vegetation types, and latitudinal range. In simple regressions, the number of island soil types was the best single predictor of island species number. In multiple regressions, area, °N latitude, and distance from Britain also made significant contributions to the prediction of island species numbers. These analyses are discussed in terms of the theory of island biogeography in general and the description of the British Isles in particular. The slope of the log species, log area curve reveals that the plant species distribution pattern on the British Isles is more like that of continents than of islands.

Introduction

In 1835, H.C. Watson observed that 'on the average a single county appears to contain nearly one-half the total number of species in Britain; and it would, perhaps, not be a very erroneous guess to say that a single mile contains half the species of a county' (from Dony, 1963). In that statement we see an early recognition that the relationship between the number of species in a flora and the area described may be made linear by use of a logarithmic scale. The first attempts to formalize this species–area relationship were made by Arrhenius (1921) and

Gleason (1922). That the species–area relation is logarithmic (curvilinear rather than linear) has been documented by numerous studies (for reviews, see Malyshev, 1969; Johnson & Raven, 1970). Dony (1963) has used this relationship to predict the completeness of British floristic studies.

The first exhaustive attempts to explain the reasons for the logarithmic nature of the species–area relationship were made by Preston (1962) and Williams (1964). From these studies two major hypotheses may be distilled. The first is Preston's, as elaborated by MacArthur & Wilson (1967) and Greenslade (1969), and states that area has an effect as follows. There is some distribution of individuals into species such that there are rare and common species, and the biota of any area is determined by a dynamic equilibrium between immigration and extinction. Further, extinction probability monotonically increases as population size decreases, and population size of course decreases as area decreases. Consequently, as one samples progressively smaller areas, more and more of the rare species will be absent. In fact, because of the mathematical nature of species-individuals distributions, the species–area relationship will be increasing not only monotonically but also curvilinearly. Simberloff (1972) has provided direct experimental evidence that area *per se* contributes to the determination of species on small mangrove islands in Florida.

The second hypothesis (Williams, 1964) is based on the premise that environmental heterogeneity increases with increasing area. As area increases, the number of habitats, each with its characteristic species, also increases, so that the species–area relationship is increasing monotonically. But as the area sampled is increased by equal increments, the probability of finding a *new* habitat decreases for each successive increment; the species–area relationship is therefore curvilinear.

Hamilton *et al.* (1963) expanded the analysis of species richness in islands (Galápagos) to include independent variables other than area. They found that the amount of island relief (elevation) and the

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degree of isolation also were correlated significantly with island species numbers. For the Galápagos and other island groups the species–elevation relationship has been linear rather than curvilinear (Johnson & Raven, 1970) in the face of a high island area-elevation correlation. The interpretation of this has been that an increase in elevation adds new habitats while an increase of area only adds to the probability of finding new habitats (Johnson & Raven, 1973). This argument may be extended to support the hypothesis that environmental heterogeneity as well as area is involved in the determination of the species-area relationship.

The British Isles have been comparatively well studied floristically and offer a good opportunity for an examination of the species–area relationship. Just as important as the rather well worked flora is the fact that important environmental parameters have also been mapped. As a result, we can look directly at relationships between species numbers on islands and the relative heterogeneity of an important environmental parameter, namely soil types. The latter have long been known to have an important effect on both plant distributions (Warming, 1909) and plant evolution (Kruckeberg, 1951). The intent of this study is accordingly to analyse relationships between soil types and island species numbers, and the general pattern of island species numbers in the British Isles.

Materials and methods

The values of ten variables for each island in the British Isles were collected from a variety of sources as listed below:

S the number of species of vascular plants on the island (Perring & Walters, 1962);

A island area in square kilometres (nautical charts, atlases and miscellaneous books);

E maximum elevation of the island in metres (as for A);

L mid-point of the latitudinal range of the island in °N latitude (taken from maps and nautical charts);

R latitudinal range of the island in degrees (as for L);

D_1 distance from mainland Britain in kilometres (as for L);

D_2 distance from the nearest other island in kilometres (as for L);

ST number of major soil types on the island (Bickmore & Shaw, 1963);

H' soil diversity on the islands calculated as $-\Sigma p_i \log p_i$, where p_i is the relative frequency of the ith soil type. The values of p_i were determined with a planimeter (as for ST); and

VT number of major vegetation types on the island (as for ST).

Only about half of the islands where values of S could be determined are used in the analyses. Islands not used are those where the species lists may be less than 80% complete and/or where the values for other variables could not be found. Of the independent variables, elevation is the usual piece of missing information. Data for the islands are given in Table 1.

Latitudinal range (R) was selected on the grounds that for islands of the same size, species number would be greater for any island whose shape and arrangement gave that island greater latitudinal range. The increase in species number would be predicted because an increased latitudinal range provides an increased number of environments. For the British Isles, this variable proved empirically to be of little value because of its almost perfect correlation with area ($r_{A, R} = 0.991$). Similarly soil types (ST) and vegetation types (VT) are redundant. The distance from the nearest other island (D_2) is the minimum shore to shore distance. When a very small island is the nearest island to a larger one, the nearest other island is taken to be the nearest island with a flora large enough to make a significant contribution to immigrating species. These subjective judgments were used only in a few instances. The source flora is considered to be that of Britain since nearly all species in the British Isles are found on that island. We consider this to be a reasonable approximation for ecological time, the time scale of importance here, but not for evolutionary time.

We hypothesized that an island with several soil types where one type predominates and the others are rare will be likely to have fewer species than an island with the same number of soil types, all of which are equally abundant. We therefore calculated H' (which increases with both an increase in ST and a tendency toward equal abundance of soil types) to test this hypothesis. The soil H' did not add to the analyses when ST was used and did not correlate as well as ST with S when used alone. Since we used a very general soil classification, each soil which appeared on an island probably occurred over a large enough area to support the species characteristic of that soil. The soil H' may be of more value if a more detailed classification of soils were used.

Table 1. Raw data and regression predicted species numbers for islands included in this study

Island	A Area (km)^2	E Elevation (m)	ST Soil types	L Latitude (°N)	D_1 Distance from Britain (km)	S Observed species no.	$\hat{S}$ Predicted species no.
Ailsa	0·8	340	1	55·3	14·0	75	38
Anglesey	712·5	127	3	53·3	0·2	855	959
Arran	429·4	874	4	55·6	5·2	577	503
Barra	18·4	384	2	57·0	77·4	409	337
Bressay	31·1	226	1	60·1	201·6	177	177
Britain	229849·8	1343	16	54·3	0·0	1666	1816
Canna	12·7	210	1	57·1	40·6	300	203
Coll	74·1	103	3	56·6	14·5	443	379
Colonsay	44·8	143	1	56·1	31·1	482	512
Eigg	29·0	393	1	56·9	12·3	453	593
Fair	5·2	217	1	59·5	143·5	174	162
Fetlar	40·9	159	2	60·6	246·8	189	119
Foula	13·5	418	1	60·1	177·4	149	204
Gigha	15·5	101	1	55·7	3·4	401	427
Hoy	154·1	477	2	58·9	13·1	354	248
Iona	9·1	101	1	56·3	37·1	388	350
Islay	605·3	490	3	55·8	22·4	581	490
Jura	379·4	784	3	56·0	4·8	444	492
Lewis	2137·3	800	5	58·1	38·2	527	458
Lundy	4·1	144	1	51·2	18·1	338	302
Man	571·6	620	3	54·3	29·0	765	917
May	0·5	51	1	56·2	9·0	137	260
Mingulay	9·6	272	1	56·8	85·5	269	232
Muck	5·4	137	1	56·8	8·5	284	338
Mull	909·6	967	4	56·5	2·1	517	488
N. Ronaldsay	7·3	15	2	59·4	85·5	131	184
N. Uist	305·6	347	3	57·6	57·1	433	302
Orkney	489·5	269	6	59·0	28·1	440	463
Rona	10·4	123	1	57·5	6·5	159	146
Rhum	106·7	810	3	57·0	24·8	425	533
Sanday	50·2	66	3	59·3	62·9	162	215
Shetland	984·2	450	6	60·3	188·7	421	390
Skye	1735·3	1009	5	57·3	0·6	594	585
S. Ronaldsay	60·9	119	2	58·8	9·7	207	163
S. Uist	365·2	620	3	57·2	82·3	470	474
Stronsay	35·2	45	2	59·1	51·5	62	21
Tiree	76·4	140	2	56·5	36·8	378	391
Unst	121·2	285	2	60·8	258·1	246	2
Westray	55·4	170	2	59·3	66·1	65	22
Whalsay	19·7	120	1	60·4	221·0	158	78
Wight	380·7	238	3	50·7	1·6	1008	964
Yell	217·3	205	2	60·6	235·5	161	133

By reasons of hindsight given above, VT and H' were eliminated from Table 1 and all analyses. Additionally R and D_2 are eliminated from Table 1 and most further analyses.

Using S or log S as the dependent variable, three classes of regression analyses were computed: (1) linear (data untransformed); (2) data log-transformed (curvilinear of Hamilton *et al.*, 1963); and (3) mixed (one or more variables log-transformed and one or more variables not log-transformed). Both simple and multiple regression analyses were computed for all three classes.

Results

The correlation coefficients between analysed variables are given in Table 2 for both raw and log-transformed data. The independent variable most highly correlated with island species numbers relates

Table 2. Correlation coefficients for variables analysed. The upper triangular half-matrix is for raw data and the lower triangular half-matrix is for log transformed data

	Area A	Elevation E	Soils ST	Latitude L	Range R	Distance from Britain D_1	Distance from nearest island D_2	Species number S
A	1·000*	0·508	0·841	−0·199	0·991	−0·131	−0·125	0·695
E	0·628	1·000	0·594	−0·192	0·574	−0·234	0·047	0·626
ST	0·896	0·506	1·000	−0·150	0·893	−0·177	−0·023	0·774
L	−0·115	−0·159	−0·089	1·000	−0·186	0·705	0·110	−0·606
R	0·915	0·521	0·863	0·003	1·000	−0·133	−0·100	0·727
D_1	−0·147	−0·111	−0·143	0·637	−0·099	1·000	0·159	−0·400
D_2	−0·154	0·089	−0·047	0·115	−0·205	0·352	1·000	−0·092
S	0·692	0·567	0·563	−0·572	0·572	−0·414	−0·145	1·000

* The critical values of r for significance levels are: $r = 0·3044$, $P = 0·05$; $r = 0·3932$, $P = 0·01$; $r = 0·4896$, $P = 0·001$.

Table 3. Summary of simple regression analyses with S or log S as the dependent variable

	Linear			Log transformed			Mixed		
x*	r^2	P	x	r^2	P	x	r^2	P
A	0·4836	<0·001	log A	0·4790	<0·001	log A	0·5912	<0·001
E	0·3921	<0·001	log E	0·3214	<0·001	log E	0·2669	<0·001
ST	0·5991	<0·001	log ST	0·3174	<0·001	ST	0·3064	<0·001

* x, independent variable; r^2, coefficient of determination; P, significance level of regression coefficient (t-test).

to the number of island soil types, followed by latitudinal range, area and elevation. The results of the more important simple regression analyses are given in Table 3. It is worth noting that latitudinal range does have a high correlation with island species number. However in the multiple regression analyses R did not make a significant contribution to the estimation of S. In this study we find for the first time an independent variable (ST) which predicts island species number better than does area.

The results of some of the multiple regression analyses are given in Table 4. Many more such

analyses were computed with various combinations of independent and dependent variables, but those listed produced the greatest coefficients of determination. For the linear regression, the number of soil types, island latitude and the distance from Britain are the significant contributors to the determination of island species numbers. In the other analyses, island area may also be a significant contributor, sometimes to the exclusion of the number of soil types. The mixed analyses in general give a greater prediction of S than either the linear or curvilinear analyses.

Table 4. Summary of stepwise multiple regressions with S or log S as the dependent variable

Dependent variable	Independent variables included	Independent variables ($P < 0·05$) making a significant contribution to the regression (F-test)	R^2
S	All not transformed	ST, L, D_1	0·8639
log S	All log transformed	log A, log L	0·7492
S	Log A, remainder not transformed	ST, L, log A, D_1	0·9098
S	ST, remainder transformed	ST, log L, log A	0·9117
S	All variables and their transforms	ST, log L, log A, log ST	0·9479
log S	Log A, remainder not transformed	log A, D_1	0·5941
log S	ST, remainder transformed	log A, log L	0·7434

With respect to the species–area relationship, there are two basic differences between the British Isles and other island groups which have been studied. First, the slope of the $\log S - \log A$ curve is 0·209, with an estimate of 0·238 using multiple regression analysis. The theoretical slope given by Preston (1962) is 0·26. Similar estimates of $\log S - \log A$ slopes for the Galápagos are 0·313 and 0·370 (Johnson & Raven, unpublished); and for the California islands (Johnson, Mason & Raven, 1968) 0·370 and 0·378. The slope is accordingly considerably lower for the British Isles. Secondly, the correlation between S and A is not improved for the British Isles data by log-transformation as it is for all other similar studies.

Hamilton *et al.* (1963) suggested that islands which are small or distant will have higher residuals (the difference between the regression-predicted S and the observed S) than islands which are near or large. The same observation was made for the California islands (Johnson & Raven, 1970) for island size, but the opposite was true for distance. The correlation between A and D_1 for the Galápagos study of Hamilton *et al.* is $-0·28$ and for the California islands $+0·38$. The value of r_{A, D_1} for the British Isles is nearer zero. A test of the relationships between area and distance respectively, and regression residuals, was made in this study by computing the correlation coefficients between the absolute value of the residual and A and D_1. The correlations were low and statistically insignificant. The values of S predicted from the regression are summarized in Table 4 (line 4), and are given in Table 1.

Discussion

The slope of the $\log S - \log A$ curve for the British Isles suggests a pattern more characteristic of continents than islands. As has been pointed out by Preston (1962) and MacArthur & Wilson (1967), values below the predicted slope of 0·26 are expected for continental samples. On continents, some species collected in an area may be transients. The presence of these transients reduces the number of new species encountered with increasing area, as compared to islands where isolation greatly reduces the number of transients. The mainland areas sampled in California (Johnson *et al.*, 1968), for example, have a $\log S - \log A$ slope of 0·158 and a multiple regression estimate for the slope of 0·176.

In terms of geological history the British Isles have long been considered to be continental islands (Darlington, 1957); the land bridges disappeared about 7000 years ago. For an island group to maintain a continental $\log S - \log A$ slope the immigration rate (addition of species/unit time) must remain high and/or the extinction rate (loss of species/unit time) low. With the large size of the islands and the short inter-island distances that occur in the British Isles, such rates would be predicted.

The correlation matrix and simple regression analyses offer clear evidence of the importance of soils in determining island species numbers. We have shown that area may be correlated to island species numbers because it is an index of environmental heterogeneity (ST in this case). Clearly one can argue that ST and S are correlated because of a fortuitous correlation between A and ST. We can counter that ST is a better predictor of S than is A and therefore is the more proximal cause. Further to this point, we can only state that we have evidence strongly supportive of the hypothesis that environmental heterogeneity contributes to floristic wealth and that this is reflected in turn in the species–area relationship. The proof of this we must leave to the ingenious scientist who can design the critical experiment.

Our multiple regression analyses reveal also the significance of isolation (D_1) and latitude (L) in decreasing island species numbers. The latitudinal effect is the commonly observed gradient. In this case it is most likely the result of the effect of temperature on floristic wealth. An alternative effect, related to the linear north–south orientation of the islands with the predominant link to the continent in the south, might be considered for the British Isles; however, our interpretation of the $\log S - \log A$ slope as consistent with Preston's prediction does not support the alternative, leaving us in favour of the temperature hypothesis.

Hamilton *et al.* (1963) suggested the use of mixed regression analyses in studies such as these. While these proved successful here for the first time, their importance lies not so much in the determination of which form of analysis might produce the best prediction of S, but in the determination of which environmental variables show a significant relationship to S and in the clarification of the mathematical nature of that relationship (linear *v.* curvilinear, etc.). From these observations we may generate and sometimes test hypotheses concerning the general problem of floristic wealth. We urge that future

floristic studies, particularly of islands, include further analyses of the type presented here.

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