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Numbers of plant species on the islands of Aldabra Atoll

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The logarithm of island area accounts for 70% of the variance in the number of plant species occurring on 100 lagoon islands. Two components of island altitude (altitude of the island rim and the logarithm of the island's inland altitude) are also of importance, and account for 9% of the variation in species numbers. A further 13 variables account for only an extra 5% of the variance in the mixed model. These results resemble the findings of other island studies. In the equation $S = KA^z$, $z = 0.345$ and falls within the range of expected values.

The species–area curve gives little indication of the 'small island effect' found for other small islands; this may reflect, among other factors, the richness of the Aldabran flora when compared with those of the small island ecosystems already studied. The curve is also compared with that compiled by Williams (1964) and a discrepancy between the two is discussed.

Woody plants are largely responsible for the increase of species numbers with increasing area. Species that are restricted to islands of particular sizes are listed and the characteristics of the frequencies of occurrence of the more common species are summarized.

Introduction

The study of island floras and faunas has formed an important part in the formulation of biogeographical theory (see, for example, MacArthur & Wilson 1967; Carlquist 1965, 1974). Many studies have attempted to elucidate the factors that determine the number of species occurring on islands, particularly the number of plants and of birds, and island area has usually been found to predict species number better than any other variable. The equation $S = KA^z$, where S is the number of species on an island, A the area, and K and z are constants, describes the general form of the relation between species number and island area. In some cases, however, area is not the best predictor of species number and some other factor has been found to provide a better indication of environmental diversity. For example, Hamilton, Rubinoff, Barth & Bush (1963) found that, by using a linear model, island altitude is the best predictor of plant species number in the Galápagos; and in the British Isles, the number of soil types per island predicted plant species number better than area (Johnson & Simberloff 1974). Latitude has been shown to be of some importance (Johnson, Mason & Raven 1968; Johnson & Simberloff 1974; Power 1972), and Abbott (1974) showed that plant species number on 19 sub-Antarctic and nearby islands were influenced more by the temperature of the coldest month of the year than by area.

In addition to the above variables that describe the habitat diversity of an island, there are others that relate to an island's potential for receiving immigrants. They include such factors as the isolation of an island from potential sources of immigrants and the richness of the source area. These factors are generally less important in determining species number than those describing island environmental diversity (see, for example, Abbott 1974; Hamilton *et al.* 1963; Johnson *et al.* 1968; Johnson & Simberloff 1974).

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Aldabra Atoll (lat. 9° 24′ S, long. 46° 20′ E) consists of nearly 2000 islands, of which four large ones enclose a lagoon studded with many smaller ones. It is the smaller islands that are the focus of this study. They were formed from a single land mass when, 4000–5000 years ago, the atoll rim was breached by the sea, and lower-lying land within the rim was flooded (Braithwaite, Taylor & Kennedy 1973). Some of the islands have probably formed since then by erosion of the lagoon shores of the islands forming the atoll rim. The vegetation of the islands is derived from that on them when they were formed, plus immigrations, minus extinctions. They support a proportion of the approximately 250 species that make up Aldabra's terrestrial flora. They are situated in a lagoon measuring 30 × 10.5 km and none is more than 1060 m from the next island. They are low (mean altitude 1.44 m, range 0.25–8.50 m) and, but for a few sandy keys, consist almost entirely of limestones that compose the raised reef system of Aldabra. Soil is generally scarce and shallow, except for a few areas of deep sand. Thus, the main respect in which the islands differ from one another is in area, which was expected to account for most of the variation in species number. It was, however, deemed useful to include as many as possible of the factors that might affect species number so that their relative statistical importance could be determined.

Methods

(*a*) *Variables*

Lists of the vascular plant species on 100 lagoon islands and the four large islands that form the atoll rim were made during 1973 and 1974. For the lagoon islands, estimates of the frequency of occurrence of each species were made during the wet season.

Measures on 19 independent variables were included in the analysis of determinants of plant species number. They consist of 12 that have been considered in other studies and seven others of potential importance.

(1) *Area.*

(2, 3) *Altitude.* This was considered as two components: the altitude of the island rim, that is, its shoreline above the high water level at spring tides (2), and the altitude from the top of the rim to the highest point inland (3).

(4) *Distance to nearest lagoon island.* This provides a measure of the island's isolation.

(5) *Distance to the nearest large island forming the atoll rim*, which was regarded as being the 'mainland' within the atoll ecosystem; another measure of the island's isolation.

(6–12) *Rock type*, as distinguished by Braithwaite *et al.* (1973). The types that were found on the islands consist of Picard Calcarenites (6), Esprit Limestone and Phosphorites (7), Takamaka Limestone (8) and Aldabra Limestone (9), as well as cavity fill (10) and beach deposits (11). A few islands consist partly or wholly of sand (12). In the absence of information on soil types for Aldabra, rock type provided the best available indication of the nature of the substrate on which the plants grew. As estimates of the proportions of each island composed of different rock types were unreliable, only presence or absence of a particular type was used in the analysis.

(13) *Percentage of the island on which soil occurred.*

(14) *Mean depth of soil.* Measures of variables (13) and (14) were obtained in the course of recording the incidence of plant species within 1 m^2 quadrats.

(15) *Presence of potholes.* It was thought that potholes might provide a sheltered microhabitat

with deeper soil than elsewhere on an island and that this might influence plant species number. Presence or absence of potholes was used in the analysis, as estimates of the abundance of potholes on each island could not be made reliably.

(16) *Distance to the nearest pass between the sea and the lagoon.* The passes represent the routes by which seaborne seeds originating from outside the Aldabran ecosystem would reach the lagoon islands; the nearer an island to a pass, the more likely it is to intercept foreign seeds.

(17) *Distance to Grande Passe.* As the largest of the atoll's passes and so the most likely route of entry of seaborne material, distance to Grande Passe was considered separately from the others.

(18, 19) *Position of the island in the lagoon on an east–west axis* (18) *and on a north–south axis* (19). As the main islands of the atoll rim show some geographic variation in the occurrence and abundance of plant species, it was thought that this variation might be apparent in the number of species on the lagoon islands as a function of position in the lagoon rather than as the result of any other factor.

A copy of all these data has been deposited with the Aldabra Data Recording Scheme at the Department of Geography, Downing Place, Cambridge CB2 3EN, U.K.

(*b*) *Selection of islands*

An island was defined as a piece of land that was always above high water level, even at the highest spring tides, and that was separated from all other pieces of land by every high tide. With the exception of a number of islands between La Gigi and Pointe Tanguin, for which data were collected in the course of developing the methods used in the study, the islands were selected on a restricted random basis. The guiding principle in choosing islands was to have as wide a range as possible of variation with respect to the independent variables. Large islands and islands isolated from one another and/or from the 'mainland' are relatively rare; all such islands were therefore included. The remaining islands were chosen randomly from the following areas: the eastern end of the lagoon, east of a line passing from Passe Houareau to a point at grid reference E 30, N 07; the eastern end of Ile Malabar; the group of islands south of Ile Esprit; and the islands south of Ile Polymnie. The only islands without representation in the study were those south of the middle and western portions of Ile Malabar.

(*c*) *Analysis*

Stepwise multiple regression was used to determine which of the independent variables were most important in determining species number on islands; the program employed was part of the Statistics Package for Social Sciences. The regressions were run on both untransformed and log-transformed data, and a mixed model was then constructed, using for each independent variable whichever of the linear or logarithmic variables accounted for the greater part of the variance.

Results

Sixteen variables account for 84.16% of the variance in the number of plant species on the lagoon islands. From table 1, it can be seen that $\log_{10} A$ is by far the most important determinant of plant species number, although island altitude also contributes considerably to the total variance. The higher the island rim, the greater is the number of plant species supported by the island, whereas it is the logarithm of the inland altitude rather than the untransformed values, that shows a higher correlation with species number. These relations suggest that, once a certain height above sea level is reached, increased altitude is of less significance, presumably because the influence of sea water, either through wind-borne spray or percolation through the rock, diminishes. The presence of sand on an island has a small, but significant effect on the number of plant species present, probably because it provides a different environment from the limestones. The presence of Picard Calcarenites presumably increases the

TABLE 1. VARIABLES IN THE MIXED MODEL THAT CONTRIBUTE TO MORE THAN 1% OF THE VARIANCE IN THE NUMBERS OF PLANT SPECIES ON LAGOON ISLANDS

variable	percentage of variance for which variable accounts
$\log_{10} A$†	69.75**
$\log_{10} a$†	6.55**
altitude of island rim	2.87**
presence of Picard Calcarenites	1.39*
presence of sand	1.23*

**, Significant at $p < 0.01$, one-tailed; *, significant at $p < 0.05$, one-tailed.
† A, area; a, inland altitude.

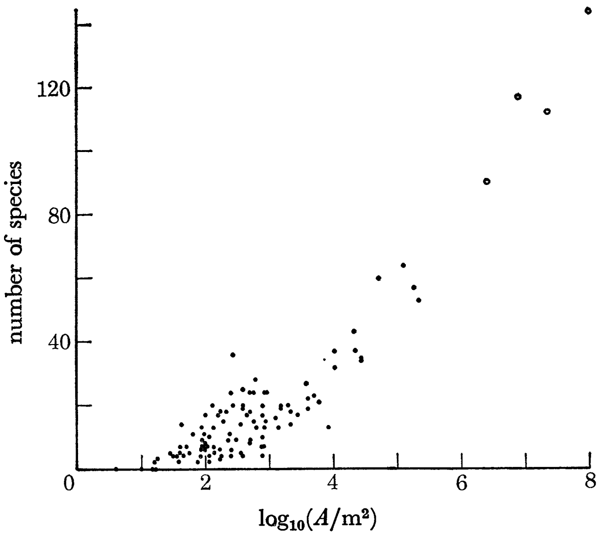

FIGURE 1. Number of plant species plotted against $\log_{10} A$. ○, Data for the large islands of the atoll rim.

number of plant species for the same reason, although it is not known what characteristics of this limestone type are particularly favourable to species diversity. None of the variables describing the isolation of the lagoon islands is of statistical importance; this is perhaps not surprising given the small distances between islands, and between islands and the 'mainland' of the atoll rim.

In the mixed model shown in table 1, $\log_{10} A$ accounts for 69.75% of the variance in the number of plant species (n) per island. If, however, area is to be used as a single variable in predicting species number, a better estimate is obtained by using $\log_{10} n$ and $\log_{10} A$, in which case $\log_{10} A$ accounts for 78.84% of the variance. The nature of the species–area relation is

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shown in figure 1. The curve climbs more steeply as $\log_{10} A$ increases but the regression coefficients for the lowest ($\log_{10} A < 2.0$) and highest ($\log_{10} A > 4.0$) portions of the curve are not significantly different from one another. Data for the four large islands of the atoll rim were not used in the multiple regression analysis because of their probable incompleteness but, as shown in figure 1, the points for these islands lie on the same curve as the lagoon islands. A plot of $\log_{10} n$ against $\log_{10} A$ (not illustrated) shows an almost linear relation for areas up to about 3.0 with a much less sharp increase in $\log_{10} n$ for the larger islands, including those of the atoll rim.

In the equation $S = K A^z$, $z = 0.345$.

In table 2 (see microfiche), where a mixture of physiognomic and taxonomic criteria are used to provide a convenient classification of the components of the island floras, it is shown that all elements of the floras contribute to the increased number of species with increasing area. Kruskal–Wallis one way analysis of variance indicates that the mean numbers of each type of plant are significantly different on islands of different sizes. The number of woody plant species increases more rapidly with area than the other categories of plants, suggesting that the major difference between large and small islands lies in the variety of woody plants that they support.

Examination of the species lists for the islands indicates that there are critical size limits for the occurrence of many species. Most of these species are, as expected, confined to the larger islands, but a few species of herbs and grasses are found only on the smaller islands. Table 3 (see microfiche) summarizes, for species of restricted occurrence, the sizes of islands on which they typically occur. The 52 species listed in table 3 represent nearly half of the 116 species of plants found on the islands; of the other 64 species, 35 occur on islands of all sizes and 29 are found rarely and show no clear preference for islands of particular dimensions.

Further information on the habitat requirements of individual species can be gained from the mean frequency with which they occur on islands belonging to the five $\log_{10} A$ classes. The mean frequencies were calculated for those islands on which the species occur, provided the species are found on 10 or more of the 100 islands studied. As shown in table 4 (see microfiche), the grasses tend to occur with greatest frequency on the smallest islands, with frequencies declining through the log area classes of increasing size. Of the 14 herbs that grow on 10% or more of the islands, 9 show the same pattern as the grasses, but only 4 out of 19 woody plants do. From these figures, it can be seen that grasses and herbs are relatively common on small islands while shrubs are generally rarer on smaller than on larger islands. This picture bears out that obtained from the presence–absence data of table 3. It was expected that the frequency of occurrence of woody plants would increase with increasing island area, but this was found to be true for only three species. The majority of woody plants either showed peak frequencies on intermediate island sizes or, more rarely, varied little over the range of island areas studied. It would appear that, for all but three species, factors other than area are also important in determining their prevalence, although what these factors are have still to be established.

Discussion

With the exception of the sub-Antarctic and nearby islands studied by Abbott (1974) and the British Isles (Johnson & Simberloff 1974), A or $\log_{10} A$ has been found to be the most important factor predicting plant species diversity on islands (references quoted in table 5 (see microfiche)). Hamilton *et al.* (1963), working with a linear model for the Galápagos islands' plants, found that altitude accounts for more of the variation in species number than area. However, when log-transformed data are used, $\log_{10} A$ is more important than any other variable, a view that Johnson & Raven's (1973) study with more recent data confirms. For Aldabra Atoll too, area is the most important variable in linear (66.68%), logarithmic (78.84%), and mixed (69.75%) models. As table 5 shows, the percentage variances in species number accounted for are comparable to values found by others. The two measures of island altitude together account for 9.4% of the variation in the number of plant species on Aldabra's lagoon islands, a figure very similar to that found for the low, sandy, northwest Hawaiian islands by Amerson (1975).

The value of z for Aldabra's lagoon islands is higher than that predicted from theoretical considerations for islands (Preston 1962), but is within the extremes of 0.15–0.39 reached by May (1975) from general considerations. At 0.345, it is not greatly different from values for the plants of the Galápagos calculated by Johnson & Raven (1973) and Preston and those for the Californian islands (Johnson *et al.* 1968). It has been suggested that high values of z can be expected for isolated areas (MacArthur & Wilson 1967), and the relatively high z for Aldabra may be taken to reflect its isolated position, 650 km off the east African coast and 390 km northwest of Madagascar. However, the reported values of z for land plants on true islands are similar (range 0.31–0.37), despite the varying degrees of isolation of the different islands. This observation supports Tepedino & Stanton's (1976) suggestion that z varies with the organism under study.

MacArthur & Wilson (1967) have drawn attention to the fact that, on very small islands, species number tends to remain constant over a range of island areas. They suggest that catastrophic events frequently denude such islands which therefore have area-independent extinction rates among their floras and faunas. While this may be true for some islands, such as the Florida Sand Keys, the 'small island effect' on Kapingamarangi Atoll is better explained by the observation that below an area of 1.42 ha or, more particularly, with an island width of less than 107 m, an island is probably not large enough to maintain a lens of fresh water (Niering 1956; Whitehead & Jones 1969). In the absence of such a lens, the only plants that establish on the islands are strand species, of which there are a limited number. The species–area curve for Kapingamarangi Atoll thus has an inflexion point at around island area of 1.42 ha, the curve climbing more steeply with islands of larger areas as non-strand species make their appearance.

As few of the species found on Aldabra's lagoon islands are introduced, a comparison can be made of Aldabra's species–$\log_{10} A$ curve (figure 1) with that for Kapingamarangi Atoll from which introduced plants are excluded. Aldabra's curve, like that for Kapingamarangi Atoll, climbs less steeply with increasing area among small than among large islands. There is, however, no significant difference between the flattest and steepest sections of Aldabra's curve. In fact, when the two curves are plotted on the same scale, the lower section of Aldabra's curve is seen to climb very much more steeply than the comparable section of Kapingamarangi's and there is no clear inflexion point in Aldabra's curve, although it is definitely steeper for areas greater than 10^4 m^2 (*ca.* 1 ha) than for smaller island areas. In other words, it appears that Aldabra's lagoon islands show only weakly, if at all, the small island effect. Furthermore, the entire curve for Aldabra's islands is displaced to the left of Kapingamarangi's, suggesting that Aldabra's islands support more species area for area than the sandy keys of Kapingamarangi.

They also support more species than the northwest Hawaiian islands (Amerson 1975) and the limestone islands west of Perth, Western Australia (Abbott 1977). Amerson quotes a mean of 3.6 species of vascular plants on islands with a mean area of 2.3 ha and a mean altitude of 2.4 m, and Abbott found that islands less than 4615 m^2 in area tend to be devoid of plants.

The difference of Aldabra's islands from these others may be explained in various ways. The Aldabran ecosystem may be floristically richer than these others because of its greater size and, in the cases of Kapingamarangi and the northwest Hawaiian islands, its lesser isolation from source areas of colonists. The temperature and rainfall régimes on Aldabra are probably more favourable for the evolution and maintenance of plant species diversity than those of Kapingamarangi and the Western Australian islands. The lagoon islands are sheltered from strong winds and heavy seas, and cyclones rarely reach Aldabra. These more sheltered conditions make it unlikely that the islands will be affected at all frequently by catastrophic events. Thus, while Amerson found that an island needs an altitude in excess of 1 m to support one species of plant, and Abbott that islands lower than 3.3 m tend to have no plants on them, many of the Aldabran islands with lower altitudes have more than one species. Furthermore, large colonies of nesting birds, which destroy the vegetation and reduce the number of plant species present, are found on only 10 % of the islands studied.

The upper section of the curve in figure 1 is a straight line, showing that the four large islands of the atoll rim have the same species–area relations as the lagoon islands. Comparison of the same data, on a log–log plot, with Williams's (1964) generalizations about the characteristics and interpretation of the species–area curve leads to an interesting conclusion. Williams found that, when $\log_{10} n$ is plotted against $\log_{10} A$, the first part of the curve rises steeply and then flattens out; he suggests that this curve corresponds to what is expected of species number within a single ecological association. At areas of about 4–8 ha ($\log_{10} A$ = 4.6–4.9), the curve rises more steeply again, indicating the inclusion of new environments. The Aldabran curve shows the first steep climb followed by some flattening out, but there is no evidence of the second sharp rise. The absence of the second steep climb in the curve suggests that Aldabra's flora may be seen as forming one ecological association. This conclusion appears reasonable for the flora of most of the lagoon islands, but not for such islands of the atoll rim as Grande Terre where the platin formation provides a distinctive habitat characterized by tortoise turf (Grubb 1971), which is not found on the lagoon islands. One may question whether the inclusion of new habitats, as area sampled increases, necessarily shows up as an increase in $\log_{10} n$. On Aldabra, the mixed scrub that covers most of the atoll is species rich by comparison with the tortoise turf. Inclusion of the tortoise turf adds relatively few extra species to the total species count and does not show up in a log–log plot.

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Microfiche

The relevant frames of the microfiche included with this publication contain the following tables referred to in the text of this paper.

Table 2. Mean number and range of plant species per island on islands of different sizes

Table 3. Species with occurrence restricted to islands of certain sizes

Table 4. Change in mean frequency of occurrence of species in quadrats on islands of different sizes

Table 5. Comparison of the percentage variation in numbers of vascular plant species on islands accounted for by area and altitude in this and other studies