

Patterns of species diversity among the Seychelles islands

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Abstract

A comparison of the relationships between species number and island area or height indicated that height is the best predictor for molluscs and amphibians. This is probably due to the relationship between island height and rainfall or habitat diversity. Other taxa (birds, plants and reptiles) give inconclusive results following from incomplete data, unidentified extinctions or ongoing colonisation.

Introduction

Patterns in the numbers of species of animals and plants occurring on islands or in habitat patches are frequently explained by the theory of island biogeography relating species number to island area (MacArthur & Wilson 1967). Several more recent studies, particularly those pertaining to plant numbers on islands in the Great Barrier Reef (Heatwole 1991) have identified other variations on this theme centering on island height - species number relationships. To date there have been few attempts to apply island biogeography theory to the islands of the western Indian Ocean. Previously published studies have included birds (Diamond 1984) terrestrial molluscs (Peake 1971) and amphibians (Nussbaum 1984). Recent advances in the thoroughness of species lists have resulted in a great increase in the volume and accuracy of data available for such applications for fauna and flora of the Seychelles island group. Data are presented below for the land mollusca, reptiles, amphibians, birds and plants and the resultant relationships discussed in terms of ecological saturation, recent extinction and the contribution made by introductions. The numbers of species of various taxa are compared to island area or height using data from Nussbaum (1984) (amphibia), Cheke (1984) (reptiles), Robertson (1989) (plants) and Gerlach (1994) (snails). Pearson's correlation tests were used to identify significant correlations between species numbers and the area or height variables. Both raw data and log transformed data were used.

Results

The results of these comparisons are shown in Table 1. Reptiles and plants from the corraline islands are considered in more detail in Table 2. In all tables significance levels of correlations are given as:

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

Table 1. Pearson's correlation

	all islands				granitic only			
	area	log area	height	log height	area	log area	height	log height
amphibia	0.46**	0.63***	0.97***	0.79***	0.72***	0.94***	0.96***	0.78***
log amphibians	0.35**	0.56***	0.90***	0.86***	0.57*	0.88***	0.87***	0.85***
reptiles	0.36**	0.52***	0.76***	0.85***	0.48	0.71***	0.74***	0.85***
log reptiles	0.32**	0.49**	0.64***	0.88***	0.39	0.62**	0.65**	0.89***
plants	0.76***	0.82***	0.75***	0.46	0.87***	0.88***	0.86***	0.55*
log plants	0.41	0.64**	0.40	0.38	0.45	0.68**	0.62**	0.48
snails	-	-	-	-	0.87***	0.92***	0.97***	0.69**
log snails	-	-	-	-	0.71***	0.90***	0.95***	0.85***
land snails	-	-	-	-	0.82***	0.91***	0.97***	0.68***
log land snails	-	-	-	-	0.67**	0.88***	0.90***	0.73***
native snails	-	-	-	-	0.83***	0.92***	0.97***	0.71***
log native snails	-	-	-	-	0.69***	0.89***	0.94***	0.85***
birds	-	-	-	-	0.65*	0.90***	0.77*	0.80**
log birds	-	-	-	-	0.63*	0.89***	0.77**	0.82**

Table 2.

	area	log area	height	log height
reptiles	0.389	0.445	0.466*	0.469*
log reptiles	0.341	0.396	0.448	0.423
plants	0.492*	0.548*	0.676**	0.582**
log plants	0.749***	0.791***	0.845***	0.806***

This comparison shows that for all the islands the most significant interactions are:

amphibia - height
log reptiles - log height
plants - log area

for granitic islands only:

amphibia - height
log reptiles - log height
plants - log area
snails - height (for all snails, terrestrial snails, terrestrial native snails)
birds - log area

and for coralline islands only:

reptiles - log height
log plants - log height

The variables are combined in Table 3. in order to identify cases where area and height combine as predictors of species number.

Table 3.

		Variables		First variable		Total	
		1	2	r ²	F	r ²	F
all islands	amphibia	height	log area	0.934	564.55***	0.937	289.89***
	log reptiles	log height	log area	0.453	32.28***	0.532	21.57***
	plants	log area	height	0.670	81.06***	0.766	63.89***
granitic	amphibia	height	log area	0.920	230.34***	0.951	184.40***
	log reptiles	log height	log area	0.500	20.07**	0.516	10.11**
	plants	log area	height	0.783	72.11***	0.792	36.16***
	snails	height	area	0.942	179.18***	0.968	152.62***
	birds	log area	log height	0.780	31.96***	0.800	14.006**
coralline	reptiles	log height	log area	0.220	4.80*	0.236	2.46
	log plants	log height	log area	0.339	9.24*	0.457	7.14*

Discussion

The combination of variables shows that in all cases addition of a second variable does increase the explained variance (r^2) but reduces the significance of the regression, the second variable is thus not a helpful addition. For the amphibia the full data set provides the best regression due to the numerical dominance of the small, low islands which do not support amphibia. Reptile species number is associated with island size but the extremely low r^2 values indicate the importance of other factors in determining numbers. What these other factors might be is not clear, but may include ongoing active colonisation of the islands. Interestingly reptile diversity is very poorly correlated with island size on the coralline islands, which would be expected to be the first to be colonised by new species immigrating from source populations in the Malagasy region and thus may not exhibit any clear biogeographical patterns. This possibility of ongoing colonisation affecting the regressions has also been suggested by Gardner (1986) who also cites several recent colonisation events (such as *Mabuya sechellensis* to Bird and Denis islands and *Phelsuma* spp. to several of the Amirantes in the last 100 years).

Plants correlate reasonably well with island size, area being the predominant influence. This breaks down when the coralline islands are considered in isolation; the primary influence being log height which only explains 34% of the variance. Snail diversity is almost entirely explained by island altitude.

Niche filling

According to the theory of island biogeography the curve of species number - island size for stable communities should take the form

$$S = CA^z$$

with $z = 0.27-0.35$. For the groups studied above the following are obtained

	z
log all reptiles = 0.17 log height + 0.41	0.17
birds = 6.10 log area + 7.72	0.17
snails = 0.06 height + 0.22	0.41
all amphibia = 0.13 log height - 0.08	0.45
all plants = 137.23 log area + 8.85	0.72

Thus on theoretical grounds alone it would appear that the numbers of reptiles and birds observed are much lower than their theoretical stable value whereas amphibians and snails are slightly above the stable value with plants being greatly in excess. This has some support when the biogeographical properties of the different groups are considered. As suggested above the low significance of reptile regressions may be due to ongoing colonisation.

The data set analysed above gives a significant result for granitic island birds and area in contrast to the findings of Diamond (1984) for native birds, however Diamond (1984) reported a significant result for the total avifauna. The z value is improved in this analysis (rising from Diamond's 0.12 for natives to 0.17), they may remain below a stable value due to extinctions caused by human disturbance. To test this possibility two further regressions were tested. For the first the minimum number of species recorded on each island was used and for the second widespread distributions were assumed giving each island several of the species that have not been recorded there historically:

	z
restricted range	0.17
generally assumed fauna	0.17
widespread	0.22

The widespread model gives the most stable value of z which may indicate that the original avifauna of Seychelles was more uniformly distributed between the different islands than is usually assumed. It may also indicate that we do not know of all the extinctions that occurred after human colonisation. In accordance with this uncertainty a research project into subfossil deposits on the granitic islands is planned.

A similar data manipulation improves the fit of the snail data; using only species numbers for presumed native species gives $z = 0.39$ which is marginally less than the original value, however the original may be better as it is identical to that of the amphibians where none of the species are believed to be introduced.

The best fitting regressions and most stable numbers are produced by amphibians and snails, both of these are very strongly associated with island height due to high humidity requirements (high islands tending to have highest rainfall values). Both these faunal elements are largely comprised of vicariant species that must have been present since the islands were isolated from India 65 million years ago (92% of amphibians and at least 50% of molluscs), thus colonisation is only a limited component of the recent biogeographical history of these two groups. This

is not the case with the plants where the majority of the fauna is composed of species that have arrived relatively recently, many introduced by human activity, this un-natural component may be the cause of the elevated numbers of species producing a z value over twice the theoretical maximum.

Height or area ?

The most interesting associations are those between amphibians or snails and island height. The usual variable is area, height may be a more significant factor for two reasons; it is a good predictor of rainfall which is an important influence on certain taxa (eg. amphibians and snails) and is also associated with habitat diversity. There is insufficient data on rainfall from most islands to allow the significance of this component to be evaluated. Habitat diversity data are similarly scarce, a comparison of regressions using the available data on the numbers of habitat types on each island (using the classification of Gerlach 1993) indicates that habitat diversity is correlated with island height:

height:

$$\text{habitat} = 0.02(\text{height}) + 1.95 \quad r^2=0.86 \quad F=83.26 \quad P<0.001$$

area:

$$\text{habitat} = 0.06(\text{area}) + 3.07 \quad r^2=0.30 \quad F=17.53 \quad P<0.001$$

The area regression is also significant but explains only a third of the variance. More data from a greater range of islands are needed to refine these relationships and to investigate the details of the associations.

This evaluation of the currently available data identifies several problems that obscure the precise nature of the relationships. It would be expected that significant regressions would be obtained between plants and area for the coralline islands as has been found in most other island groups (Heatwole 1991; Williams 1982), this was not found, probably due to considerable variations in the completeness of plant lists for the different islands. The problems with the bird data have been discussed above. The problems with these two data sets indicate the need for the compilation of complete species inventories and an investigation of the limited subfossil deposits. The latter should allow more reliable estimation of the numbers of plant and animal species that were lost following human colonisation.

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