

The Application of Island-Biogeographic Theory to Patches of Habitat: How Much Land is Enough?

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ABSTRACT

The problem of estimating the minimum-sized parcel of land needed to preserve a given suite of species is little-addressed. Two techniques available for such estimations are: (1) 'the method of island biogeography', which uses extrapolations of the species–area equation; and (2) 'the method of addition', which uses only the actual suite of 'islands' under investigation. No rationale exists for choosing technique 1 a priori, although the choice is often made. The two techniques produce minimum area estimates which define a spectrum of potential minimum areas. Determination of the real minimum area requirement must rely upon detailed natural-historical observation.

INTRODUCTION

Traditionally, the construction of nature refuges has had no particular 'strategy'. Areas have often been protected as a matter of convenience or compromise, rather than as a result of biological considerations. A major reason for this situation was that no general guidelines were available to aid conservationists in determining the best structure of refuges. Recently, however, equilibrium island biogeographic theory has been advanced to fill this gap (Diamond, 1975; May, 1975). Various aspects of the theory predict that refuges should be large, close, circular, etc. (see Diamond, 1975). Although such generalisations are appealing, they are not without their critics. Biogeographers have questioned both the prediction that one large refuge is necessarily better than several small

ones of equal cumulative area (Helliwell, 1976; Simberloff & Abele, 1976; Higgs & Usher, 1980) and that circular refuges are necessarily better than ones of other shapes (Game, 1980). I have noted previously that predictions derived from the equilibrium island biogeographic model are specious when the model's assumptions are not met (McCoy, 1982). It remains to be determined how seriously such criticisms compromise the model's predictive power in general. How accurate the model is in estimating appropriate morphologies of refuges probably varies among situations. Higgs (1981), for example, has demonstrated how both the slope of the species-area regression and the proportion of species in common between patches of habitat aid in deciding between one large or several small refuges. Even with such refinements, the resulting estimate of proper refuge design may be far from realistic. Confidence in this strategy of nature refuge design seems to have waxed and waned in a rather short period of time, and the call for particular examination of individual situations is increasingly common (Simberloff & Abele, 1976; Higgs, 1981; McCoy, 1982).

It is strange that the controversy outlined above has focused nearly entirely upon the morphology of individual refuges, when such is rarely the chief concern of conservationists. More often, the conservationist is faced with choosing between various immutable parcels of land. The typical way in which the choice is made is by censusing each parcel as thoroughly as possible and preserving the one with the largest list of species or that with the most endangered species. A critical question, then, is: can the minimum-sized parcel needed to preserve a certain suite of species be determined? This question has received virtually no critical attention to this point; thus, it is important to determine how effective island biogeographic theory and other approaches might be in answering it.

CALCULATING MINIMUM AREA

In equilibrium situations in which habitat heterogeneity does not vary appreciably among patches, an appropriate way to determine minimum refuge area is to use the species-area equation (MacArthur & Wilson, 1967; Connor & McCoy, 1979) as a species-accumulation curve; i.e., to extrapolate the curve to the number of species to be preserved, and note the corresponding area value. Species richness can be influenced by

environmental variables other than area, however, and this fact often produces substantial variation about species-area regression lines. Prediction of richness by means of area is risky. I contend that simple extrapolation of the species-area equation is inappropriate in many situations, and that minimum refuge area likely is over-estimated as a result. I illustrate the problem by contrasting two techniques for predicting the minimum amount of land required: one I term 'the method of island biogeography', which consists of the extrapolation process described above; the other 'the method of addition', which consists simply of calculating the minimum area that actually contains the number of species to be preserved in the suite of 'islands' under investigation. These two methods are explained best with a hypothetical example.

First, assume that the species of, say, land birds residing on a certain 15-island archipelago are distributed among the islands as a function of area; and that the relationship is described by the realistic equation:

$$\log S = 0.70 + 0.20 \log A$$

One archipelago that satisfies this assumption is illustrated in Table 1, and is used in the following analysis. Next, assume that the total number

TABLE 1
The Number of Species, the Areas, and the Log-Transformations of These Variables for the 15 Islands in the Hypothetical Archipelago

<i>Island</i>	<i>log S</i>	<i>S</i>	<i>log A</i>	<i>A</i>
1	0.74	5	0.2	1.58
2	0.78	6	0.4	2.51
3	0.82	7	0.6	3.98
4	0.86	7	0.8	6.31
5	0.90	8	1.0	10.00
6	0.94	9	1.2	15.85
7	0.98	10	1.4	25.12
8	1.02	10	1.6	39.81
9	1.06	11	1.8	63.10
10	1.10	13	2.0	100.00
11	1.14	14	2.2	158.49
12	1.18	15	2.4	251.19
13	1.22	17	2.6	398.11
14	1.26	18	2.8	630.96
15	1.30	20	3.0	1 000.00

TABLE 2

(A) The Total Amount of Area Necessary to Hold the Entire Species Pool of 30.^a (B) The Results of an Analysis Identical to the First Run in (A), Above, but with the Species Pool Set at 120

(A) Pool size = 30			(B) Pool size = 120	
Cumulative area of islands	Cumulative number of species		Cumulative area of islands	Cumulative number of species
	Run No. 1	Run No. 2		
1.6	5	5	1.6	5
4.1	11	7	4.1	11
8.1	15	9	8.1	17
14.4	16	10	14.4	22
24.4	19	10	24.4	29
40.2	25	15	40.2	38
65.4	26	18	65.4	42
105.2	29	20	105.2	50
168.3	30	20	168.3	56
268.3	—	26	268.3	63
			426.8	70
			678.0	77
			1 076.2	83
			1 707.0	88
			2 707.0	95

^a The method for obtaining these data is described in the text. The first run allows all species potentially to colonise all islands. The second run allows the first ten species to colonise only five of the islands, the second ten to colonise these five plus an additional five, and the last ten to colonise all 15 islands.

of land bird species which are potential colonists of the archipelago is 30; and draw randomly, with replacement, from these 30 to determine the species composition of each island (i.e., island 1 receives five randomly chosen species, island 2 receives six, etc.). Finally, beginning with the smallest island, accumulate species occurrences until all 30 species in the pool are included. This procedure is illustrated in Run No. 1 of Table 2A.

The result of the analysis is that the entire species pool is contained on 168.3 area units, given a random distribution of species among islands (see Coleman, 1981). This estimate of minimum area was produced by the method of addition. It should be pointed out that the estimate is conservative: it is possible that the entire species pool could be contained on a set of islands of total area less than the area of the *N* smallest islands

required to hold the pool (see the real example, below). The method of island biogeography, i.e., extrapolation of the species–area regression, indicates that more than 6000 contiguous area units are needed to hold the entire pool. Practically, it would be a less formidable task to attempt to conserve 168.3 units than more than 6000.

Even though the above situation is perfectly reasonable, I have made a substantial number of arbitrary decisions in constructing it: (1) the size of the species pool; (2) the species–area equation; (3) the total number of islands; (4) the areas of the islands; and (5) the type of species-distribution (random overlap). What would be the effect on my result of having decided differently?

The size of the species pool

Table 2 illustrates the effect on number of species accumulated of employing a relatively small or a relatively large species pool (if all islands are filled, our archipelago can accommodate between 20 and 170 species). When the species pool is set at 30 (Run No. 1 of Table 2A), only 168.3 area units (cumulative area of the nine smallest islands) are required to accommodate all 30 species; but when the species pool is set at 120 (Table 2B), 2707 area units (cumulative area of all islands) accommodate only about 80% of the species. It must be kept in mind, though, that extrapolation of the species–area regression to $\log S = 2.08$ requires $\log A = 6.90$, which is nearly five million area units. As long as the slope of the regression equation is less than 1, the rate of increase in area will exceed the rate of increase in number of species, meaning that the absolute difference in the amount of area required to contain the entire species pool according to the two methods will increase with increasing pool size.

The species–area equation

Increasing the slope of the line to, say, 0.40 effectively increases the number of species of birds resident on each island (for instance, for the equation $\log S = 0.70 + 0.40 \log A$, the smallest island in our archipelago would contain six species and the largest 79 species). Using a 120-member species pool, we find the larger number of species per island results in a larger cumulative number of species contained on less cumulative area: i.e., increasing within-island diversity reduces the total area necessary to accommodate the species pool. Such is true regardless of which of the two

methods of calculating minimum area is employed. However, the difference between the methods noted in (1) above remains.

The total number of islands

Assume that the archipelago is enlarged by adding islands to the sequence illustrated in Table 1 (i.e., $\log A$ of island 16 = 3.2, etc.). The effect of increasing island number on species accrual then depends upon the size of the species pool. Increasing the number of islands in the archipelago either can have no effect (for relatively-small pools) or increase the number of species accommodated (for relatively-large pools). Note, however, that the rate of acquisition of new species relative to area by the method of addition is faster than that obtained by extrapolating the species-area curve, no matter how islands are added.

The areas of the islands

Assume that the areas of the 15 islands in the archipelago are those in Table 1, but each is multiplied by a series of constants. Increasing the size of the smallest island is then equivalent to decreasing the species-pool size, as above, producing the same results.

These simple calculations show that more information is needed about the resident species than the simple observation that their richness is a function of area. Given this, virtually nothing can be said about the minimum area needed to preserve the entire pool. We must have data on turnover rates, pool size of potential colonists, etc. But, even more crucial is the need for sound autecological observations on the species studied. This is illustrated vividly by considering the importance of the species-distribution in determining the amount of land required to hold the entire species pool. Recall that the analyses performed to this point have assumed that species are assigned to islands randomly and independently. If such a situation does not obtain (for instance, if some species of large-bodied birds can survive only on the very largest islands), the entire species pool will require a larger minimum area for its continued existence (compare Run No. 2 in Table 2A with Run No. 1). In fact, the smaller the subset of islands available to each species, the larger the cumulative area required. Obtaining substantial information on the 'niche' (*sensu lato*) of each species is thus of utmost importance.

It appears, then, that the two methods described above may produce

results near the ends of a spectrum of potential minimum areas. This conclusion suggests that no reason exists *a priori* for choosing one end (that produced by the method of island biogeography) preferentially over any other point in the spectrum, given practical constraints on the amount of land that can be preserved. Such a choice is often made, however. Consider an example.

Shreeve & Mason (1980) tabulated the number of butterfly species present in 22 woodlands of various sizes in eastern England. The number of species present was significantly positively correlated with the area of the woodland. To predict the area necessary to support the 26 species of butterflies found in all woodlands combined, the authors simply extrapolated the species–area curve derived from their data. They determined this value to be 458 ha.

Shreeve & Mason (1980) extrapolated their species–area regression based upon the assumption that ‘single, large woods are more valuable for the maintenance of a high diversity of species than a number of smaller woods of an equivalent area in close proximity’ (p. 418). This assumption is not supported by any natural-historical or population data on the butterflies, nor even by the authors’ own analysis: all 26 species actually could be found in a mere 180 ha of woodland (Table 3). For these butterflies, the minimum area likely lies somewhere between 180 and 458 ha.

It should be noted that a very critical question (perhaps the most critical one) is not addressed at all by this sort of analysis: are any of the woodlands more ‘important’ than others, regardless of size? In the study above, for instance, Lineage Woodland (only 85 ha, Table 3) contains 22 butterfly species (about 85 % of the total fauna), including 5 that are ‘rare’ (found in 3 or fewer of the 22 woodlands). Is this an important woodland in preserving the regional fauna, out of proportion to its diminutive size? Is it more important in this respect than Markshall Woodland, which is nearly twice as large but contains only 18 species, none of which is rare by the criteria listed above? The difference between these two woodlands in terms of butterfly species richness indicates that area may not be the best criterion to employ in designing a refuge. Perhaps differences in habitat structure between forest patches are great, largely overriding the influence of area. It may also be that these butterfly species are not at all restricted to woodlands, and the method of island biogeography is misapplied in this case (see McCoy, 1982). Once again, the critical, but absent, information is detailed data on both the woodlands and the butterflies.

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