COLONIZING ABILITIES, ISLAND SIZE, AND THE NUMBER OF SPECIES ON ARCHIPELAGOES

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One of the ideas that has emerged from the dynamic view of island biogeography (MacArthur and Wilson 1967) is that lessons about the design of wildlife refuges may be drawn from an island metaphor. The design of wildlife refuges may be divided into two stages, colonization and extinction. The colonization stage may be regarded as the initial decision to set aside particular parcels of land. The extinction stage is the gradual loss of species from the refuge through time. Most applications of island biogeography theory to wildlife refuge design have centered on the extinction stage; how might extinction rates be minimized in a refuge? The prediction has been made that large wildlife refuges are needed in order to preserve as much of the natural fauna as possible (Terborgh 1974; Diamond and May 1976). This result has helped generate a favorable atmosphere for setting aside wildlife refuges large enough to preserve much of the faunal diversity.

Simberloff and Abele (1976) noted that under certain assumptions the species area relation $S = cA^z$, when generalized to more than a single island, predicts that more species will be found on two small islands than on a single large island with the same or even larger area. They present field evidence to demonstrate that, at least in one case, the number of species on an island that had been fractionated into an archipelago increased. They argue that a conservation scheme involving several small refuges may preserve more species than a single large refuge. This argument pertains to the colonization stage of wildlife refuge design. This argument was criticized by a number of investigators (Diamond 1977; Terborgh 1977; Whitcomb et al. 1977) on several grounds. (1) A system of small refuges may not preserve those species which require a minimum area or population size for survival. (2) Small refuges will be less likely to preserve all trophic levels. (3) Extinction would proceed more rapidly in the set of small refuges. (4) Fragmentation of available refuge area is an irreversible strategy.

While all of these arguments are cogent, none deals explicitly with the effect that Simberloff and Abele observed. Here I examine the conditions under which several small islands, habitat patches, or wildlife refuges will contain more species than a single large island, habitat patch, or wildlife refuge. I shall show

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that the effect noticed by Simberloff and Abele occurs only when the total refuge system contains a very small fraction of the species to be preserved or when biologically implausible assumptions are made about the species. Thus, fragmentation of a potential refuge, even taking into consideration the effect of Simberloff and Abele, might be the wrong management strategy.

I shall first discuss the relation of the number of species on a single island to the number of species on an archipelago. I first assume that all species have identical colonizing abilities and then modify this assumption to include the more biologically realistic property of differing colonizing abilities. In the second portion of this paper I discuss the effect of immigration between islands and immigration from the mainland on the species composition of an archipelago.

I. COLONIZATION

In order to develop some basic models to predict the number of species in an archipelago, several quantities must be defined:

S_S, S_L = the number of species on a small and a large island, respectively.

S_T = the total number of species on an archipelago of n islands.

A_S, A_L = the area of a small and a large island; $RA_S = A_L$.

P = the number of species in the species pool on the mainland.

The simplest model of colonization assumes that all species have identical colonization abilities and that assortment of species onto islands is random. Assume that the number of species is related to the area of the island by the Arrhenius species-area relation (Preston 1960), $S = cA^z$. Here z is a constant in the neighborhood of .25 (May 1975; Sugihara 1981). Then,

$$S_L = c(RA_S)^z \qquad S_L = R^z S_S. \qquad (1)$$

The probability that any given species from the species pool is found on the small island is S_S/P. The probability that any given species is not found on the small island is $1 - S_S/P$. The probability that it is not found on n small islands is $(1 - S_S/P)^n$. Thus, the probability that a given species is found on at least one of the n islands is $1 - (1 - S_S/P)^n$. Because this model assumes that all species in the species pool have equal colonizing abilities, the expected total number of species on n small islands is

$$S_T = P[1 - (1 - S_S/P)^n]. \qquad (2)$$

One can now phrase the question that Simberloff and Abele raised in analytical terms. When will a group of small islands have more species than a single large island? When is $S_T > S_L$? From equations (1) and (2),

$$P\left[1 - \left(1 - \frac{S_S}{P}\right)^n\right] > R^z S_S$$

$$\frac{S_S}{P} < R^{-z}\left[1 - \left(1 - \frac{S_S}{P}\right)^n\right]. \qquad (3)$$
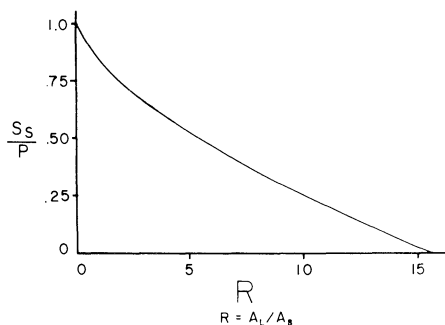
FIG. 1.—Plot of the relationship $S_L = S_T$ given by expression (3) as a function of the size ratio of a small and a large island, and the number of species on the small island. Above the line a single large island will have more species than a pair of small islands ($n = 2, z = .25$).

A graph of $S_L = S_T$ is shown in figure 1 for two small islands, $n = 2$, and $z = .25$. Above the line $S_L > S_T$ there will be more species on a single large island; below the line $S_T > S_L$ there will be more species on two small islands. For $R > n^{1/z}$ (or 16 for $z = .25$) no value of S_S/P, however small, can satisfy the relation $S_L < S_T$. However, there is a large range of values for S_S/P and R for which there are more species on an archipelago than on a single island.

From the standpoint of conservation and the design of wildlife refuges one wishes to preserve as many species as possible. One would like S_T/P to be as close to one as possible. The requirement that S_S/P be lower than some critical value in order that the condition $S_T > S_L$ be met seems at odds with the attempt to preserve as many species as possible. Such a requirement, while not crucial under the current assumption, becomes critical if one relaxes the assumption of identical colonizing abilities.

I shall now alter the assumption of identical colonizing abilities. Diamond (1974) and Simberloff (1978) have demonstrated that species vary widely in their dispersal or colonizing abilities. If some species are inherently better colonists than others, one would expect most islands to have on them the very good colonists and few islands to have the very poor colonists. Two islands composed of species with different colonizing abilities would be expected to show a greater degree of faunal similarity than one might expect of two islands composed of randomly collected groups of species. Because the faunas of the two islands would be similar, one would expect fewer total species to be found on both islands together.

In defaunation studies of small mangrove islands (Wilson and Simberloff 1969; Simberloff and Wilson 1969) three species (the phyticid moth *Bema ydda*, the chrysopid *Chrysopa rufilabris*, and the curculionid beetle *Pseudocalles* sp.) appeared on four of the six defaunated islands in either the first or second sampling period. Two other species (the blattid cockroach, *Latiblatella* n. sp. and *Chrysopa collaris*) appeared on three of the six islands within the first two sampling periods. Considering a species pool of approximately 500 species (Simberloff 1976) and the fact that these five species made up 21 of 67 species occurrences in the first two

sample periods, the immigration abilities of mangrove arthropods must be highly skewed.

What is the underlying distribution of colonization abilities? This distribution is largely unknown for any group of species. However, if colonizing ability were proportional to the number of propagules produced, one might expect a lognormal distribution of colonizing abilities. If the colonizing ability of a species is the sum of a large number of species-specific characters which independently affect colonizing ability, one might expect a normal distribution of colonizing abilities. Regardless of the actual form of the distribution of colonizing abilities, some species will be vastly better colonists than other species. One may approximate the range of variability in potential colonizing ability by varying the single parameter of the geometric model. The probability that the next colonist is of the ith most dispersive species is

$$q(1 - q)^i. \tag{4}$$

I justify the use of the geometric model on the grounds that (a) it captures much of the variability one might expect from more complicated models, (b) it is a single-parameter model and (c) the single parameter has a simple biological interpretation, i.e., it is the probability that the next colonist will be of the most dispersive species.

The geometric model with large values of q (greater than .5) is a very uneven distribution and is in one sense the direct opposite of the assumption of equal colonizing abilities. However, the effects discussed below do not require this extreme unevenness. For the small values of q that are discussed in this paper (in the neighborhood of .01–.10) the geometric model is a very even distribution. That is, for any given species, those of similar rank will have very similar colonizing abilities. It is sufficient to note that a moderately good fit to lognormal distributions of rank-colonizing ability may be obtained with a geometric model, as illustrated in figure 2. At the same time the geometric model provides a better description of differential colonizing abilities than the unrealistic assumption of equal colonizing abilities.

The geometric series converges to 1 as i goes to infinity. However, with a finite species pool of P species, the value given by expression (4) must be normalized to one as

$$\frac{q(1 - q)^i}{1 - (1 - q)^P}. \tag{5}$$

The expected number of species on an island after m colonization events is

$$S_{\text{geometric}} = \sum_{i=0}^{P} 1 - \left(1 - \frac{q(1 - q)^i}{1 - (1 - q)^P}\right)^m. \tag{6}$$

Figure 3 shows the relation between the total number of species on two islands, S_T, as a function of the number of species on one of the islands for various values of q. As colonizing abilities become more disparate, with increasing values of q, the overlap in species composition between two islands increases and S_T becomes smaller.
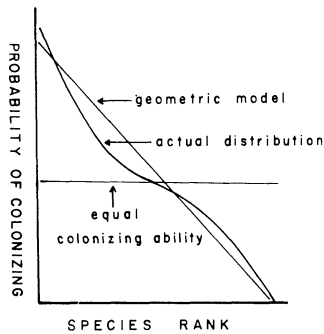
FIG. 2.—A rank-colonizing ability plot. The probability of colonizing is plotted on a logarithmic scale against the species rank, in a fashion analogous to a rank-abundance diagram. The geometric distribution can provide a better fit to an actual modal distribution than can the assumption of equal colonizing abilities.
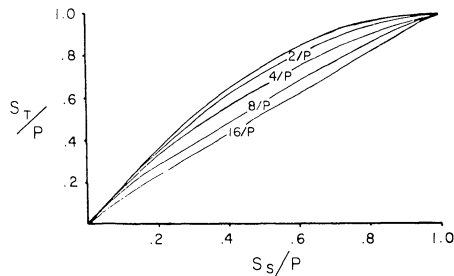

FIG. 3.—Number of species on an archipelago of two islands as a function of the number of species on one of the islands. The top line is the curve expected from the assumption of equal colonizing abilities; other curves are expected for colonization described by the geometric model with the given paramenter. As colonizing abilities become more disparate (q increases) the total species on the archipelago approaches the number of species on one island.

For conservation one wishes to preserve as many species as possible. Preservation of 80% or $.8P$ of the fauna will be designated in this paper as a minimally effective refuge. Two small wildlife refuges would be established instead of a single large refuge only if such refuges preserve more species than a single large refuge. If the two small refuges are each one-half the area of the large refuge and species relations are linked by equation (1), then in order for $S_T > S_L$, $S_T > R^z S_S$ or $S_T > 1.19 S_S$ (for $z = .25$). Figure 4 shows $S_T = 1.19 S_S$ superimposed on the values of S_T given by the geometric colonization model for various values of q.

For two small islands to have more species than a single large island, the total number of species on the archipelago must be fewer than a critical value. These values are shown in table 1 for various assumptions about colonizing ability. With increasing values of q, the planning decision to use two small refuges in place of a single large one can be made an arbitrarily bad one. In a minimally effective refuge, one with $.8P$ of the total fauna, the value of q must be less than about $4/P$. Unless one is able to demonstrate that a given set of species has an unusually high
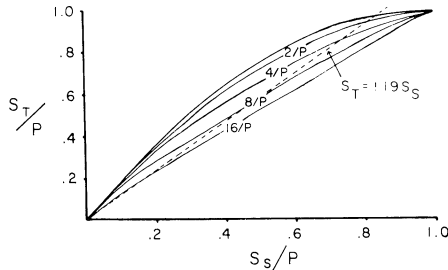
FIG. 4.—Same as fig. 3. The dotted line $S_T = 1.19S_S$ has been superimposed. Island pairs to the right of the dotted line will contain fewer species than a large island of equal total area.

TABLE 1

MAXIMUM FRACTION OF SPECIES POOL WITH MORE SPECIES ON AN
ARCHIPELAGO THAN ONE LARGE ISLAND

Type of Colonization Ranking	Highest Colonization Probability (y-intercept)	$S_{T\text{crit}}$ (% of P)
Equal	$1/P$	96%
Geometric	$q = 2/P$	92%
	$q = 4/P$	82%
	$q = 8/P$	51%
	$q = 16/P$	23%

degree of uniformity in colonizing abilities, a single large preserve will be more effective than several small ones.

At the opposite extreme, two very small islands which together contain a small subset of the total fauna (S_T small) will contain more species than a single large island, even for extremely skewed colonizing abilities. The archipelago which Simberloff and Abele studied contained $S_T \simeq .1 - .2P$ species. For virtually any distribution of colonizing and dispersal abilities, two small islands will, under these circumstances, have more species than will one large island. Even if the distribution of colonizing abilities of mangrove arthropods is as skewed as it appears from a gross analysis, one would expect the combination of very small islands, such as those studied by Simberloff and Abele, to have more species than a single large island. The other side of this observation is that a series of small refuges would not be a viable conservation strategy for this system because this phenomenon exists only for very small islands.

The community dynamics of a spatially heterogeneous, patchy, environment may be governed by the twin processes of dispersal between patches and local within-patch extinction. If individual patches are small, or if the habitat is ephemeral to such an extent that it never becomes saturated with species, any individual patch may have only a small fraction of the total fauna. Such being the case, the
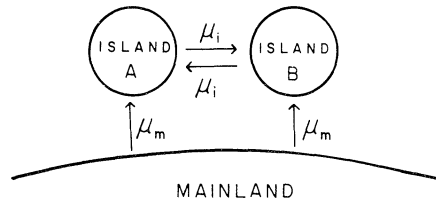
FIG. 5.—A schematic illustration of the process of mainland-island and interisland species exchange.

enhancement of species number on a complex of habitat patches may be important for a complete understanding of the organization of the community, the persistence, or coexistence of species.

II. FAUNAL INTERCHANGE

Until now I have been extolling the virtues of the island metaphor of wildlife refuges. There is an obvious area in which this metaphor breaks down; in the assumption that both colonization and extinction are taking place in wildlife refuges. Wildlife refuges should be designed to be self-sufficient units capable of preserving as many species as possible when the "mainland" source no longer exists. I shall examine the effects of allowing mainland-island colonization to take place along with island-island colonization and contrast this to the situation in which colonization from the mainland does not occur.

The situation considered in this section is shown schematically in figure 5. Two islands are each being colonized by species from the other island with probability μ_i and from the mainland with probability μ_m. For ease of calculation I return here to the assumption of species with equal colonizing abilities. The same reasoning may also be applied, with some technical difficulty, to more than two islands.

If D is the number of species that are found on only one of the two islands, one notes that the larger D is, the greater will be the total number of species in the archipelago, S_T. If the two islands are perfect complements of one another, each will have $\frac{1}{2}D$ of the species unique to the archipelago. The condition which must be met for $\frac{1}{2}D$ to be at equilibrium is

$$\tfrac{1}{2}D\mu_i = (P - S_T)\mu_m.$$

That is, the decrease in $\frac{1}{2}D$ as the result of interisland immigration must be equal to the increase in $\frac{1}{2}D$ resulting from the immigration of new species from the mainland. The assumption of equal colonizing abilities implies (from eq. [2]),

$$\frac{S_T}{P} = 2\frac{S}{P} - \left(\frac{S}{P}\right)^2, \quad \text{and}$$

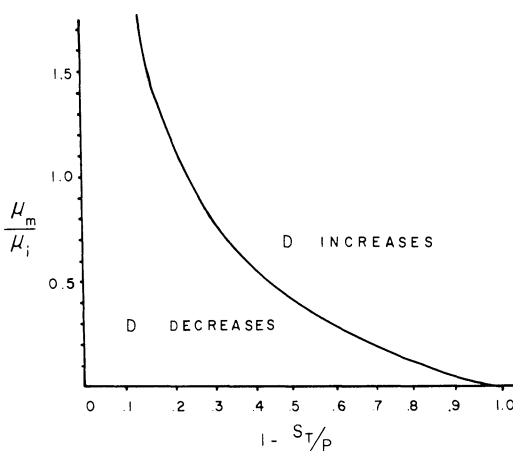$$\tfrac{1}{2}D = \frac{S}{P} - \left(\frac{S}{P}\right)^2,$$

FIG. 6.—Plot of the relationship between the relative magnitudes of immigration (μ_m/μ_i) as a function of the number of species on one of the islands. If the islands are small ($1 - S_T/P$ near one) a low level of immigration from the mainland can cause the composition of the islands to diverge.

which leads to the equilibrium condition of:

$$\frac{\mu_m}{\mu_i} = \frac{\sqrt{1 - S_T/P}}{1 - S_T/P} - 1. \tag{7}$$

Figure 6 shows this relationship for values of μ_m/μ_i and $P - S_T$. Above the line D will increase. That is, through time the overlap in species composition will decrease to an equilibrium value. Values below the line in figure 6 lead to an increase in the overlap between islands to an equilibrium level.

Simberloff (1978) provides an excellent example of the effect of immigration from a mainland source. The number of species shared by successive censuses of the same mangrove island declines as the censuses are separated by longer intervals. The serial autocorrelation is high for intervals of several months, but for censuses separated by 2 yr the autocorrelation disappears.

The situation represented by the correlation of censuses of a single island separated by a time interval is closely related to the situation of two islands simultaneously receiving colonists from the mainland. If a single island is turned into an archipelago, the species composition of the new islands is likely to be similar. However, with continued colonization from the mainland, the composition of these new islands may diverge. Whether the composition of the islands does diverge is dependent upon the relative magnitude of colonization from the mainland and colonization from the other islands.

The likelihood that the composition of two islands will diverge is also governed by the fraction of the species pool that is found on one of the islands. If the islands have few species, even a low level of immigration from the mainland is sufficient to make the islands behave as though they are independent of one another. The

archipelago which Simberloff and Abele studied contained approximately $.1$–$.2P$ species. A very small rate of immigration from the mainland is sufficient to cause an initially similar species composition among islands to diverge. This means that some of the difference in species composition in the islands that they studied may be a result of divergence based upon immigration from the mainland. This difference is of special importance only when the islands are quite small.

If one were to imagine two large wildlife refuges in the presence of a mainland source fauna, one would note that even a small amount of interisland immigration is sufficient to couple the species composition of one island to the other. In order to maintain whatever advantage there might be to establishing two refuges in favor of one, interisland exchange would have to be kept to a minimum.

The ultimate purpose of a wildlife refuge is to preserve species in habitat islands when the "mainland" no longer exists. When immigration from mainland to refuge islands ceases, μ_m becomes zero. Under such circumstances, the equilibrium value of $\frac{1}{2}D$ is zero. If interrefuge species exchange takes place along with extinction, then the refuges may come to equilibrium each with an identical set of S_S species. Note that this says nothing about the rate of approach to equilibrium, only that certain species, especially those with low dispersal abilities, will be lost from the refuge system.

SUMMARY

The major conclusion of this paper is that larger refuges or islands generally will preserve more species than a series of small refuges of equivalent total area. The claim of Simberloff and Abele (1976) that several small refuges may contain more species than a single large refuge is valid only for islands which contain a very small fragment of the total available species pool. Such areas are inappropriate as permanent wildlife refuges. A system of small tracts of land, such as a series of small urban parks, may be designed specifically to preserve only a small fraction of the total fauna in each park, but a large diversity among parks. Two small islands may contain more species than a single island of equivalent area as the result of one or both of two effects: (1) a sampling phenomenon or (2) a faunal exchange with a "mainland" source pool. Both effects are reduced with increasing island size and as a result of realistic assumptions about the relative colonizing abilities of species. Arguments presented in this paper suggest that the results obtained by Simberloff and Abele are not the result of taxonomic idiosyncrasy of arthropods; rather, their findings reflect the fact that the archipelago they studied contained only a small fraction of the total mangrove arthropod fauna.

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