Island Biogeography Theory and Conservation Practice

Abstract. The application of island biogeographic theory to conservation practice is premature. Theoretically and empirically, a major conclusion of such applications—that refuges should always consist of the largest possible single area—can be incorrect under a variety of biologically feasible costs. The cost and irreversibility of large-scale conservation programs demand a prudent approach to the application of an insufficiently validated theory.

Recent interest has been generated in the application of island biogeographic theory to the design of wildlife refuges, especially through a new brief by May (1), who has summarized recent studies on birds (2, 3) as a basis for specific conservation suggestions of general utility, while cautioning that current models do not incorporate potentially important biological facts. We propose that the proof of the underlying theory has not been so broad that conservation application ought clearly to follow, and that the main species suggestion (4) that refuges should always consist of the largest possible single area—need not be correct. Hooper's suggestions along the same lines (5) seem not to have been included. It is important to enlarge on Hooper's views and to present new evidence because widely publicized briefs may be adopted as canon in conservation planning without appropriate discussion.

The equilibrium theory of island biogeography applies to any system, since turnover (extinction and immigration) is a constant, given sufficient time. At issue is the equilibrium point, one can reasonably claim for some taxa and location that turnover is so slow that equilibrium will never be reached (7). In particular, data implying high avian extinction rates (8) have been impugned (9). In these high extinction rates, which are higher on smaller islands because smaller populations are more susceptible to stochastic breeding failure and mortality, that lead to the imperative that refuges be as large as possible (10). In cases where one large area is infeasible, it must be realized that several smaller areas, adding up to the same total area as the single large area, are not biologically equivalent to it; they will tend to support a smaller species total.

The same species-area relationship can be used to support large preserves, as well as to add to support of several small ones. If S = kA4 (where S is the number of species, A is the area, and k and 4 are constants, the latter in the vicinity of 0.2 to 0.35 for most taxa and regions), let us consider the following decision. We may construct either one large refuge of area A, or two small ones each of area A/2. By which plan would we preserve the most species? Each of the two small refuges would have S1 = kA4, species. If all species P in the species pool are equally adept at dispersing to and surviving in refuges, the expected total number of species in the two refuges together (species in both refuges counted once) would be 2S1 - S1/P (10). More realistically, we would hypothesize a gradient of total species number between S1, where a well-defined gradient of dispersal and survival abilities exists, and 2S1, where no such gradient exists, but where competitive interactions prevent many species from coexisting in the same refuge (11). In contrast, how many species, Smin, might we expect in one large refuge of area A? Letting z = 0.263 (a widely used value for log-normal distributed population sizes; the qualitative result does not depend on the exact value of 2).

Table 1. Relative numbers of species in one large refuge (S1) as compared to the number of small ones containing S1 species each. The P species in the regional pool are assumed to be noninteracting and equally adapted to refuge existence.

<table>
<thead>
<tr>
<th>N</th>
<th>S1 = total species in N refuges</th>
<th>Factor by which S1 exceeds S</th>
<th>Minimum fraction S1/P for which S1 &gt; S</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>(S1/P)</td>
<td>1.000</td>
<td>0.960</td>
</tr>
<tr>
<td>35</td>
<td>(S1/P)</td>
<td>1.335</td>
<td>0.991</td>
</tr>
<tr>
<td>43</td>
<td>(S1/P) + (S1/P)</td>
<td>1.440</td>
<td>0.991</td>
</tr>
<tr>
<td>53</td>
<td>(S1/P) + (S1/P)</td>
<td>1.527</td>
<td>0.999</td>
</tr>
</tbody>
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we find that \( S_1 = kA_1^b \), \( k = (2A_1)^b \), \( F = 1.200 \times S_1 \). This is less than the expected number in the two small refuges for \( S_1 \). \( F < 0.960 \), surely a refuge designed to maintain 96% of all species in a region would be considered ambiguous. Furthermore, the more (and smaller) refuges postulated as an alternative to a single large one, the more likely is the archipelago of small refuges to contain more species (Table 1). If anything, competition should exacerbate this disparity.

One of us (D.S.S.) has performed an experiment which tests this hypothesis. During autumn 1971, in five small red mangrove (Rhibophora mangrove) islands, a census was taken to determine their arboreal arthropod communities; the islands and census methods have been described (12). In December 1971, the experimental islands were each turned into a small archipelago by excavation of permanent, water-filled channels through the bases of the islands and by removal of the canopy above the channels. The width of the channels between vegetation on either side is at least 2 meters. In April 1975 a census of two of these archipelagoes, consisting of four and two islands, respectively, was taken. Earlier experiments (13, 14) suggest that a distance of 1 to 2 meters is a barrier to many mangrove colonists and that 3 years is sufficient for equilibration. The results from archipelago A (Table 2) support the contention that a cluster of small refuges might be expected to have more species than a single large one, although a single experiment cannot be viewed as strong evidence.

One need not invoke competition to explain this result; a group of investigators, whose reports have been reviewed by Levin (15) stress the theme of continued extinction and reinvasion in a patchy environment. Possibly the increased extinction rates on the individual islands in this mangrove archipelago are more than compensated for by the presence of the other islands as nearby sources generating high propagule (reproductive units) invasion rates. One can also conceive of environmental catastrophes (such as certain kinds of forest fires or contagious diseases) that could cause extinction if all conserved lands were united in one large refuge but would be inconsequential in one of a network of small refuges.

If we stop here we would be guilty of overdispersion. There is a limit beyond which subdivision produces refuges and, therefore, population sizes so small that extinction rates are greatly increased. The results from mangrove archipelago B (Table 2) of smaller islands may exemplify this principle. On demographic grounds one may predict that the increase in extinction rates with decrease in population size will be particularly acute below some "critical population size" (16). Critical population sizes must differ between species, as must the area necessary to support a large enough population to be relatively immune to fast extinction. An experiment on mangrove islands (17) confirms increasing extinction rates throughout an island for smaller islands, however, Heatwole (18) provides evidence for a characteristic "minimum insular area" for each of several reptilian taxa. Similarly the observation (19) that different birds on islands have different species-area curves and a review (20) of evidence for higher species-extinction rates for predators would support the idea that all species are not ecologically equal. This would have a clear corollary that not all species require the same conservation regime. Furthermore, since populations exist as components of larger entities, for certain species it may not be realistic to consider conservation of a species rather than a community (21).

At the other end of the spectrum of refuge sizes, one might predict that, if even small refuges have virtually all the species in the pool, then having several small refuges is not likely to increase the total number of species. Able and Patton have examined the arthropods of many neotropical coral heads and noted that, when two small coral heads are compared to one large one of equal total area, the pairs consistently contain more species (22). But two large coral heads have no more species than a single larger one of equal area. The critical value of \( S_1 / P \geq 0.175 \) separates the two for this biota. So in addition to a consideration of which species we can use to conserve, we must consider what fraction of the pool they comprise. Certainly for "fugitive" species adding up to a small fraction of a regional biota a single large refuge could be exactly the wrong strategy. Matters of cost may also be important (5), lower per-unit-area cost of larger patches of land may add to the advantages of size and continuity. It may be possible to strike a balance between the two opposing strategies by constructing corridors among a network of small refuges (23).

This is not a plea, then, for a specific conservation regime, but rather for a comprehensive autecological consideration. Terborgh concludes that tropical forest birds rarely disperse over even small unforested distances and therefore require large refuges, while the severe reduction of eastern U.S. forest has caused the extinction of at most two bird species from the Neotropical avifauna (24). Similarly, populations of some host-specific phytophagous insects are reduced by habitat fragmentation (25), but Ellen's suggestion that enormous rain forest reserves are needed for protection of many tropical invertebrates (26) may be too pessimistic in view of the well-dispersed dispersal capabilities even of flightless forest arthropods (12). In sum, the broad generalizations that have been reported are based on limited and insufficiently validated theory and on field studies of taxa which may be idiosyncratic.

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References and Notes
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