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Biogeography of the Megazoo

Biogeographic studies suggest organizing principles for a future system of wild lands.

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Increasing amounts of raw land are being required for development into farms, forests, roads, and towns. In addition, land is reserved because of its religious significance or unique beauty, or for recreation or wildlife protection. As the land dedicated to various purposes approaches the finite supply, increasing wisdom is demanded of decision-makers. Conservationists and planners find they must clarify the values to be considered in choosing among land parcels for wilderness or natural areas (*1*). This suggests that there is a need to consider national and global strategies toward which local, short-range tactics may contribute (*2*). A system of wildland reserves should ensure future diversity of plants and animals, while taking into account local demands on undeveloped or open space. In this article, we attempt to outline the requirements for a future biogeography that can satisfy these many demands.

It is the distributional aspects of biogeography that have interested the majority of ecologists in the past. Recent studies have introduced quantitative considerations of species numbers, which have added impetus to quantitative research in biogeography. New theories, developed primarily with data from oceanic islands, include frequent mention of habitat islands, which remain when patches of undeveloped land are left in the sprawl of cities over the landscape.

We employ a zoo analogy here and begin with a basic question: What collection constitutes a good zoo? This begs other questions of modern zoo practice, but the notion of collection has been prevalent until only recently. The ultimate collection would be one propagule of each species. This may be an appropriate goal for nature conservators, but it is physically unachievable because the description of all the world's living things is incomplete and extinctions occur while the debate goes on (*3*). If it is desirable to maintain plants and animals in the wild, then further complications exist. In structuring a future biogeography, the following questions must be answered: (i) Where should reserves be established? (ii) How many reserves should there be? (iii) What size should each be? (iv) How should they be interrelated?

Location of Reserves

At present, the location of wildland reserves is a chance process. In the future, raw land could be assessed so high that conservation organizations and public bodies will be hard pressed to meet tax or in lieu obligations. While active management generally is not a goal of wildland preservation, many indirect costs must be borne by the landowner. Such costs accumulate as an investment for which the public may demand protection. Park managers have had difficulty in gaining acceptance for programs that permit fire, disease, or insect outbreaks to go unchecked. And because of maintenance costs, some park systems have had to reject offers of land which did not include an endowment for management costs.

This paradox of managed wild lands must be recognized when considering the future of wildland reserves. Not only are the natural processes within a reserve not completely understood, the relationships and processes between reserves are just beginning to draw attention. If a chance process of reserve selection continues, it may produce a network of reserves that is both very expensive in terms of hidden management costs and very inefficient in terms of preserving a diversity of ecosystems. It may also produce a network in which all but a few species adapted to urban life become extinct.

Like the ark, a reserve network might be chosen to maintain one unit of each kind. The zoo solution of one sexual pair would not be likely to suffice in the wild, where larger numbers are required to ensure the success of reproduction. Emphasis on rare and endangered species has resulted in several land reserves for the protection of particular plants and animals (such as the Joshua tree, California condor, Kirtland's warbler, and whooping crane). This emphasis ignores the commoner plants and animals. Clearly, some assemblage of plant and animal species would be a more desirable goal for wildland reserves.

Categories of biological integrity above the scale of simple organisms are still debated. A typical definition of community is "an assemblage of populations of plants, animals, bacteria, and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development, and function" (*4*). It is difficult to conceive of a species existing outside of some community, however defined. It would satisfy the goals set out here to identify all the different types of communities and to reserve some of each. However, species tend to be distributed individually and the communities they form tend to intergrade continuously (*5*). Any point on the earth's land surface that is habitable is occupied by a particular community, but the chance of encountering precisely the same community (identical species composition) elsewhere is quite small. Communities may be fewer in number than species, but they are still numerous and are variously amenable to discrete classification.

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Natural Regions

Because both species and the communities they compose tend to be distributed in response to many environments, the problem may be approached by sorting the complex environments of the earth into more or less homogeneous regions with respect to physical and chemical variables. If some portion of each region is preserved, the life forms characteristic of the region may maintain themselves.

This approach is hazardous in two respects. (i) Regions that are similar in many environmental characteristics but have been separated for long periods of time may have structurally and functionally similar communities composed of very different species. Examples are found among the desert plant communities of South America, Australia, and Africa (*6*). (ii) The environmental variables—for instance, the precise geology, hydrology, soil types, and microclimate—may not be known in sufficient detail. Some attempts have been made to systematize obviously important environmental variables; examples are the world climatic systems of W. Köppen and of C. W. Thornthwaite (*7*); the North American physiographic systems of Fenneman (*8*) and (including climate) of Hunt (*9*); and the life zones of Holdridge (*10*). Kuchler (*11*) has produced maps of vegetation which add to existing vegetation a historical component which he terms potential vegetation.

These are broad classifications and, within each, many varieties remain to be systematized both spatially and temporally. Wright (*12*) pointed out that geomorphogenesis and climate are both dynamic processes which vary over time. Cycles in each constantly present new combinations of environmental variables, like soil moisture and soil temperature, which can alter the distribution of plants and, indirectly, animals. The rate of change in such processes is usually slow compared to rates of change in species composition, so a classification that fails to take into account the forces that induce variation is insufficient (*13*). Although these broad classifications are impractical for planning reserves at the species or community levels, they may be useful for identifying the larger differences in patterns within which specific reserves may be located. A suitable compromise might be a classification of potential vegetation such as Kuchler's (*11*). For the United States and southern Canada, Kuchler defined 66 potential vegetation groups which differ chiefly in major species composition. As a crude beginning for systematic preservation, at least one reserve could be allocated to each potential vegetation type. Problems arise with endemic species or very localized phenomena, and careful comprehensive studies would be required for each region to determine additional reserves for such special cases (*14*).

Relationships of Size and Distance

The equilibrium theory of island biogeography presented by MacArthur and Wilson (*15*) is based on the observation that richness is lower on islands than on mainland areas. An equilibrium is established between the rate of immigration of new species to an island and the rate of extinction of existing species on that island. The rate of immigration decreases monotonically with the distance of the island from a source of colonizers. All else being equal, a distant island will theoretically reach equilibrium with fewer species than an island closer to the source.

MacArthur and Wilson further argued that the rate of extinction decreases monotonically as the area of the island increases; all else constant, a small island will reach equilibrium with fewer species than a larger island. Then large islands close to source areas should have richer faunas and floras than small islands far from sources, combinations of varying size and distance giving faunas and floras of intermediate richness. MacArthur and Wilson made the point that this equilibrium should be of a dynamic nature; that is, the composition of equilibrium species may change over time but the number of equilibrium species should remain fairly constant.

Diamond (*16*), in a study of the avifauna of nine Channel Islands off the coast of Southern California, found that 17 to 62 percent of the species recorded on these islands in a previous survey had disappeared, and an almost equal number of new species had established themselves. Since the number of species that disappeared roughly equaled the number of new species for each island, it appeared that an equilibrium number of avian species had been reached on these islands. Diamond's data also suggest that no island supports as many bird species as an equal area of the same range of habitats would support on the mainland. The species turnover rate on any particular island was found to be inversely proportional to the species richness of that island. Similar results have been obtained for the avifauna of New Guinea and its satellite islands by Diamond (*17*, *18*); for the avifauna of Mona Island, Puerto Rico, by Terborgh and Faaborg (*19*); and for plants and insects of Puerto Rico by Heatwole and Levins (*20*). Technical criticisms of such studies have been made by Lynch and Johnson (*21*).

Simberloff and Wilson (*22*) studied six very small mangrove islands in Florida Bay. Having carefully censused the arthropod fauna of these islands, they fumigated with methyl bromide. This completely eliminated the fauna of the islands while causing minimum damage to the flora. The subsequent recolonization of each island by arthropods was closely monitored for a 2-year period. The islands recovered a fauna of very nearly the same number of species within 6 months. Many of these species were not originally present, and a high turnover of species was evident throughout the study period. Nevertheless, the attainment of an equilibrium was demonstrated; the number of species occurring per island did not increase after 6 to 9 months. In addition, the number of species present on each island before and after defaunation was inversely proportional to the island's distance from the nearest source of colonists.

Vuilleumier (*23*) studied the birds of paramo islands (areas above tree-line vegetation) in the northern Andes. He found that the number of species present on an island was directly proportional to its area. Also, the proportion of endemic species for any island was best explained by a measure of distance between islands (their degree of isolation). However, islands of varying distance from the nearest source area displayed a linear rather than an exponential decrease in the number of species present with increasing distance from the source. It was also found that the percentage endemism of an island's avifauna was unrelated to its area. Both of these findings are slight departures from island biogeographic theory.

A recent reanalysis of Vuilleumier's data by Mauriello and Roskoski (*24*) confirms the finding that the best predictors of an island's avifaunal species richness are its area and distance from the nearest source. However, these authors state that the best predictors of the percentage of endemic species are the island's elevation and degree of isolation.

Simpson (*25*) studied essentially the same paramo islands, but directed her attention toward the plant component of these communities. She found that the modern plant species diversity has a greater significant correlation with area and distance measures of the form of these islands during the last glacial period than with similar measures of their present form.

Other studies have considered small mammal species isolated on mountain vegetation in the Great Basin region of the western United States (*26*) and on coastal islands (*27*), fish species in lakes (*28*), arthropods in caves (*29*), insects (*30*), marine invertebrates (*31*), and freshwater mussels (*32*).

That the creation of islands on mainland areas can accelerate the extinction rate of species inhabiting the islands has been shown by Willis (*33*). Barro Colorado Island was actually a mountaintop until the building of the Panama Canal, when the creation of Lake Gatun surrounded it by water and it became an island in the new lake. It was set aside as a nature preserve in 1923. Since that time, 45 species of birds out of an original 209 have become extinct. No new species have taken their place. While many of the species that disappeared lived on second growth or at the forest edge and were presumably pushed out by forest growth, at least 13 species were forest types and one would expect them to be present. Since 1960, the three largest of the seven original ant-following bird species on the island have become extinct and at least one more may be facing extinction. It appears that Barro Colorado is approaching a new and lower equilibrium number of bird species because of its insularization.

Diamond (*34*) presented a method for estimating the time it will take for an area that has become insularized to attain its new equilibrium species number. An estimate, termed relaxation time, is the time in which 36.8 percent of the "surplus species" will disappear. The process is essentially complete after 2.303 relaxation times. Relaxation times increase with island size and can be in the range of a few decades for small islands to several thousand years for large islands.

Oxley *et al.* (*35*) studied the effects of roadways on the movements of small and medium-sized mammals by using capture-recapture techniques. Their findings indicate that roadways inhibit the movements of small forest mammals. The effect was not necessarily dependent on traffic volume or road surface but appeared to be most directly related to road "clearance," the distance the animal must travel between forest margins to cross the roadway. The authors suggested that divided highways with clearances of 90 meters or more may be as effective a barrier to movement as bodies of water twice as wide. They stated, "if large gene pools are important to the survival of populations of animals living under 'harsh' environment conditions, roadways may have important effects on these populations due to fragmentation of gene pools." Both Willis (*33*) and Diamond (*18*) have stressed the poor dispersion characteristics of many lowland tropical forest bird species. This is important and should be considered when roads are being planned, especially in game reserves or parks.

Size of a Single Reserve

Once a site is chosen, the size of a potential reserve must be considered. Several authors have emphasized that reserves should be large but none have provided dimensions (*1–3, 14, 36*). If constriction of habitat areas results in habitat islands with accelerated extinction rates and decreased species numbers, then there may be some transition size below which an area acts as an island and above which it acts as a continent. Above the transition size there would be no acceleration in the rate of species extinction, and the full complement of species present in the original habitat area would be retained. If this is so, then for any given habitat type, it should be sufficient to set aside an area at least as large as the theoretical "continental minimum."

Darlington (*37*), considering lizard and reptile populations in the West Indies, suggested that to divide the land area by 10 is to divide the species number by 2. Diamond (*2, 36*) employed a similar argument. His data for the avifauna of the Channel Islands of California indicate that Santa Cruz Island (250 square kilometers) has approximately one-fourth as many bird species as the California mainland of similar habitat (*16*). Applying Darlington's relationship in reverse, the area that would comprise a continental minimum in this case is Santa Cruz's area multiplied twice by 10, or about 25,000 km^2. Thus, in this case an area approximately 150 km by 150 km, if severed from the mainland, would in theory continue to behave as a continent with no appreciable drop in bird species diversity. In practice, however, very much larger areas have shown a loss of species (*18, 34*). If there is a real continental minimum (which would vary in size from habitat type to habitat type) it is not apparent from studies done to date.

The theoretical difficulties of minimum size might be avoided by choosing an empirical alternative from individual species range requirements. But this would not be approaching the problem on the basis of communities. For any habitat type, however, there are certain range-sensitive species, and if these were properly provided for there would be sufficient room for organisms that demand less space. In any sampling scheme the probability of missing the rare species is, of course, greater than the probability of missing a common species. Therefore one might look at the space requirements of rare (not necessarily endangered) species. Large-bodied carnivores are perhaps a good beginning. Being of large size and high on the trophic structure, these animals have fairly large range requirements. They may also be appropriate for analysis because they are often quite sensitive to human developments and are therefore very susceptible to man-induced extinctions.

Craighead *et al.* (*38*) estimated the grizzly bear population of Yellowstone National Park as approximately one animal per 75 km^2. Therefore, one family of bears (usually four individuals) might require 300 km^2. To avoid the immediate effects of imbreeding, another family should be added; the resultant is 600 km^2. Whether such small groups would be stable is questionable.

The long-term stability of populations of any size is a very complex problem. Willis' work on Barro Colorado (*33*) illustrates the fact that species may go extinct for no readily apparent reason. MacArthur and Wilson (*15*, pp. 68–93) approached the problem theoretically in trying to estimate the probability of a species successfully colonizing an island. Of importance are the per capita birth and death rates of the species, the size of the colonizing unit, and the carrying capacity of the island for the species. This method can also be employed to estimate the expected time to extinction of established species.

Applying these concepts to the theoretical grizzly reserve, with eight bears and an area of 600 km^2, and calculating average per capita birth and death rates from the Yellowstone data, we find that the expected time to extinction of the population is in the range 1000 to 1600 years. We have not taken into account the particular population characteristics of grizzlies, since we only want an estimate of the upper limit to the expected survival time.

While it seems certain that eight animals could not sustain normal population fluctuations for a period of 1600 years, several generations might occur before the population became locally extinct. To ensure grizzly bear survival, an area considerably larger than 600 km^2 must be set aside.

Data on wolves in the national forests suggest that, in good wolf habitat (Michigan, Minnesota, Missouri, and Wisconsin), one animal per 60 km^2 is a regional average (*39*). Pack size can vary from 2 to 18, with 8 being frequently encountered and 10 to 15 not uncommon (*40*). An area of 600 to 720 km^2 would then represent a minimum preserve for one pack. Similar data for mountain lions in good habitat (Idaho, Nevada, Utah, and Wyoming) suggest an average of one individual per 95 km^2 (*41*). Eight mountain lions would thus require 760 km^2.

The numbers we are considering are so low that the argument may appear trivial, but the areas required by these small populations occur in only a few of the wilderness and primitive areas of the western

United States. Of 89 designated wilderness and primitive areas in the United States, only 10 are larger than 1000 km^2 and 26 larger than 600 km^2. These 36 areas are found in 11 western states. There are no reserves east of the Mississippi large enough to support even the most transient of large carnivore populations. Black bear survival in North Carolina is one of many problems of this kind which might be considered under a reserve planning program.

Assuming that all ecosystems have some species analogous to the grizzly, wolf, or mountain lion, then the minimum reserve should consist of 600 to 760 km^2. The size depends on particular complements of animals and will vary from ecosystem to ecosystem. If this hypothetical area is multiplied by the minimum 66 vegetation types of Kuchler, the total is 40,000 to 50,000 km^2, or less than 1 percent of the land area of the United States.

Within a theoretical reserve of any size there is a pattern or mosaic of deviations from the dominant flora and fauna of the area. Fire, wind, disease, and predator outbreaks affect the land heterogeneously. There is probably some statistically constant measure of heterogeneity for any local biogeographic element. Wright (*12*) alluded to this problem in exhorting managers to allow natural catastrophic events to occur. For instance, if vegetated areas in the Boundary Waters Canoe Area are made too small, fire frequency is likely to drop off and windthrow is likely to increase as more edges are exposed. A different form of succession may well take place. The goal for wildland reservation should be to obtain a sizable enough sample to include a normal or average successional mosaic. Man has already profoundly affected the world's biogeography, and more of this kind of evidence is needed for improving decisions regarding location and size of wildland reserves.

Interactions Between Reserves

The variables that most influence species numbers on islands have been shown to be area and distance. Because terrestrial habitat islands are being made smaller and further apart by urbanization, Diamond (*2*) and Willis (*33*) have suggested that some linking device may be needed to connect islands into larger functional wholes. The flow of species through a corridor or along stepping-stones would balance the effects of insularization. Even very small separations can alter an equilibrium (*33, 35*).

Economic geography has dealt with a similar concept which attempts to describe the interaction of urban areas as a function of size and distance. Stewart (*42*) considered population potential for various distances from established population concentrations according to a demographic force, defined by analogy with the attractive force between two bodies in Newtonian physics; thus, the population potential would be directly proportional to the product of the populations and inversely proportional to the square of the distance between them. Zipf (*43*) and Isard (*44*) considered the number of train trips and telephone messages to a city as a function of its population and distance. The number of telephone messages, for example, was shown to be directly proportional to population and inversely proportional to the square of distance.

A similar hypothesis can be advanced for the interchange (of individuals, propagules, energy, information, and so on) between two habitat islands. Using the species-area relationship $S = CA^z$ (*15*, p. 9) where S is species number, A is area, and C and z are constants, a measure of the interaction between area A and area B may be described by $S_A S_B / d^2$.

Of course, different species or taxocenes belonging to S_A, for example, are not equally mobile; that is, they do not have equal probabilities of interacting with S_B. The hypothesis then suggests a community statistic rather than reference to species or taxocenes. If this statistic can be considered a measure of frequency of interaction and it is known that it decreases as the inverse square of the distance between arbitrarily isolated habitat islands, then some understanding of the required linkage may be gained.

A corridor would permit greater interchange between taxa for which the corridor is functional—large mammals, for example. Propagules dispersing randomly would reach low densities quite rapidly along a corridor. Although some niche dimensions may be maintained, it is unlikely that a particular species will find everything it requires as the corridor between two areas becomes longer. As some necessary resource decreases (according to the inverse square of distance), it becomes increasingly probable that the habitat will become limited for even the taxa that can control dispersal.

Although corridors between reserves may not be effective for the reasons set out—that is, to combine masses as a hedge against species extinction—they may serve as useful reserves in their own right. Being within the interactive field of two planned reserves, the corridor, of whatever surface area, will function as a preserve to a greater extent than an equivalent quantity of land outside the interactive field. In addition, the recreational and esthetic benefits of such corridors will be extremely important in years to come.

Size and Rank Relationships Among Reserves

The effect of smaller reserves (second order, third order, and so forth) was anticipated by MacArthur and Wilson (*15*, p. 44): "It appears that even minute islands can significantly enhance biotic exchange providing they are able to support populations of the species in the first place. If they are relatively large and close to the recipient island, they can increase the flow of propagules by many orders of magnitude." Perhaps the lower-order reserves could be chosen for less demanding animals than large carnivores and therefore be located closer to human settlements, where conflicts would not be great and there might be some recreational benefits.

Populations of plants and animals naturally grow and disperse. The dispersal is met by environmental resistance in the form of physical barriers (mountains, oceans, and forests) or barriers of competition where two dispersing groups encounter each other. The dilemma is solved by outcompeting or by some form of cooperation. Where forms of cooperation have developed, many different things may overlap. If the dispersal process proceeded uniformly with weak competition, the world would be populated by a small number of groups of large population size. If resistance was applied more strongly and homogeneously, a large number of small concentrations would result. If resistance was applied heterogeneously, some groups would occupy more territory than others. The balance of dispersal and resistance produces a biogeography which is a mix of a few groups that are successful and many that are less successful at finding new space for the growing population.

The distribution of concentrations in space has also concerned economic geographers. The rank-size relationship, attributed to F. Auerbach by Lotka (*45*) and applied to geographic problems by Zipf (*43*, p. 375) and Isard (*44*, p. 56), describes a particular concentration as belonging to a set of concentrations such that $rp^q = K$. That is, the rank r of a particular concentration (such as a city) of population P to the power of a constant q equals a constant. For example, in the 1940 census New York had a population of 11,690,570 and ranked first, and Boston had one-fifth as many people and ranked fifth (*44*, p. 56). The exponent q, according to Zipf (*43*, p. 375), is a ratio of diversification to unification, for our purposes analogous to species population growth (rN) opposed by environmental resistance (K). A homogenizing force of one successful population (man, for example) could theoretically eliminate all others. If resistance is felt randomly by a growing population, then $q = 1$ and a probable distribution is realized. As q approaches zero, or the resistance becomes large relative to growth or spatial dispersion, then the population for any rank is constant; that is, the distribution is uniform.

The similarity with the species-area curve, $S = CA^z$, is apparent. When area suitable for plants and animals is uniformly distributed, species number is constant, and where diversification in area exists, a diversity of species number is expected. However, the equations are not directly comparable since they consider different things. The rank-size relationship considers population number while the species-area relationship considers the number of different kinds of populations. However, diversification within the human community probably creates an analogy with species number; for example, larger cities have greater employment diversity (more environmental richness) than smaller cities.

With slight changes in the values of the exponents, the two equations can be used to simulate whole families of distributions. May (*46*) pointed out that this also holds for distribution in time. Most growth equations call for comparisons of existing numbers with a constant carrying capacity. Since the resistance to growth or the carrying capacity is heterogeneous in space, it is reasonable also to expect heterogeneity in time.

A corollary to the rank-size relationship is the central place theorem developed by W. Christaller and A. Lösch and discussed by Isard (*44*, p. 60). They suggest an inverse relationship between size of cities and the number of each size. The theory is that some areas are richer in resources than others and cities in those areas grow larger. The result is a pattern of cities which increase in number as they decrease in size; that is, there would be one of 1 million people, two of 500,000, three of 250,000, and so on. There is also a decline in distance between cities as size decreases.

If a 25,000-km² area could be considered a continental equivalent, it would be the largest reserve in a hierarchy. If a direct relationship between population and size is assumed, then according to central place theory, the expected distribution of smaller reserves would be:

2 reserves of	12,500 km²
4	6,250
8	3,125
16	1,563
32	781
64	390
128	195
256	97
512	49

The 66 areas of 600 km² suggested in the section on the size of reserves is roughly within the range derived from this separate source. This distribution probably represents a steady state (*47*).

Although this argument tends to suggest that areas of random size in random locations be selected for wildland reserves, the prior commitment of many land areas precludes some choices. The challenge remains to integrate the existing distribution of national parks and wilderness areas with a plan that will ensure the functional integrity of the world's ecosystems while land use for human purposes increases.

Summary

A system of primary wildland reserves may be required to ensure a diversity of plant and animal species in the future. A strategy for locating such reserves involves considerations of their location, number, size, and linkage. The equilibrium theory of island biogeography is a useful analytical tool for predicting future biogeographies according to the dynamics of present plant and animal distributions. Existing reserves in the United States are inadequate in size and number and are clumped in one geographic region. In a planned network there might be several levels of reserves, starting with first- and second-order watersheds of large enough size to support a stable population of large carnivores. Reserves should be distributed so that they include a maximum of the world's biological diversity. Lower-order reserves might serve as stepping-stones among which a supply of species might move as a kind of distributed storage and reintroduce themselves when local instabilities occur. This would maintain a high immigration rate to balance an extinction rate which can only increase as human settlements expand.

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