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THE SIZE OF NATURE RESERVES AND THE NUMBER OF LONG LIVED PLANT SPECIES THEY CONTAIN

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Abstract. Many plant communities are made up chiefly of long lived individuals of species adapted to persist by tolerating the particular stresses of their habitats. Such stresses might include: low nutrient levels; low water levels; extremes of temeprature; low light levels; low soil oxygen; low soil availability; waterlogging; extremes of pH; presence of salts or metals; among others. Long lived, often endemic, stress tolerating plants with specific habitat requirements are among those most appropriately protected in reserves. To help understand the role that reserve size plays in the choice and management of nature reserves for such plant communities, probability distributions for the number of species that remnants of larger habitats might contain were calculated assuming equal species abundance, equal individual size, and independent, random spatial distribution. For the inclusion of most species (99%) in a habitat remnant, adequate reserve size is achieved with relatively small reserves with space for about six times as many individuals as species. This suggests that the maintenance of habitat quality may be a more important factor than reserve size for the protection of biodiversity. Factors increasing or maintaining the species richness of an area of long lived, stress tolerating vegetation include: reduction of inappropriate disturbance; original inclusion of such individuals *in situ* in the area; endemism (an endemic may not have ever colonized an area, it may have evolved there); maintenance of habitat (including water table, air and water quality, and the natural variation of environmental conditions); and low mortality, especially from anthropogenous sources. As we still have a great deal to learn, both scientifically and socially, about maintenance of habitat quality, we should establish a large number of reserves of any size available, recognizing that inevitably many of them will fail for reasons of habitat quality.

Introduction

The species richness of an area is the number of species that occurs there. The species diversity of an area is its species richness, adjusted in some way to account for the relative abundance of these species. A basic goal of plant ecologists is to explain species richness/diversity. Most workers agree that, for similar kinds of areas, the number of species increases in a decelerating way as the size of the area increases. For areas of similar size, many theories would explain differences in numbers of species in terms of dynamic processes, such as competition, predation, colonization, exclusion, productivity, disturbance, equilibrium, growth rate, and rate of post disturbance return to equilibrium. Environmental factors differing among areas would affect these dynamic processes differently, resulting in more or fewer species. MacArthur and Wilson (1967) suggest that competition results in narrower realized niches, which allows more species to be present. Harper (1969) suggests that competition results in competitive exclusion, which would then reduce the number of species present. Connell and Orias (1964) suggest that *high* productivity is associated with many species, citing the species rich, warm, wet tropical forests as an example. Margalef (1969) suggests that *low* productivity is associated with many species, citing the cold stressed but little disturbed arctic tundra and alpine meadows as examples. The dynamics of colonization and exclusion are combined by MacArthur and Wilson (1967) with size and proximity to colonization sources to try to explain numbers of species in isolated areas. Huston (1979) presents an excellent review of these dynamic processes as explanations of numbers of species in areas of similar size but different ecologies, and suggests a synthesis.

More recently, concern of the conservation of species has given practical and political motivation to understand the factors that determine species richness, especially in the design, evaluation, and choice of reserved natural areas. This understanding is relevant to populous countries experiencing pressure to develop, especially if some of its people are sufficiently educated and cultured to recognize the importance of such reserves and if ecologically intact natural areas still exist. Italy, UK, Brazil and USA (among many others) are examples of such counties. Frequently, conflicts between development interests and conservation interests reveal the need for sound ecological theory concerning the maintenance of species richness.

Conservation advocates have argued that natural reserves should be large in order to better preserve species richness. Wilson and Willis (1975) have attempted to demonstrate this theoretically, using island biogeography theory. Although this work is often cited to support arguments for large reserves, which many of us favor for aesthetic reasons, development interests can argue that natural areas that are too small to maintain species richness could be developed without additional loss of biodiversity. Simberloff and Gotelli (1983) present an excellent analysis of the question of size of reserves and species richness in prairies and forests. They point out several serious problems with the island biogeography theory approach, most especially its inability to predict anything about richness in a constant area that has been divided into more smaller, or fewer larger, islands. In the modern conservation sense, a preserve is an island, surrounded by a sea of non-habitat, usually resulting from the anthropogeneous destruction of vegetation. Islands usually do have fewer species than equal sized areas on mainlands, even when ecological conditions on each are virtually identical. There are at least two likely explanations for this. Some of the species counted in the mainland area might be transients or visitors from other habitats who do not persist but are constantly replaced from them. Chance extinctions from the mainland area of species that could persist are recolonized more quickly from adjacent habitat than would be the case for extinction from islands.

Conservation advocates have argued to minimize disturbance (prevent forest fires, flooding, etc) to protect species. In some cases, disturbance may be harmful, but appropriate disturbance may be an essential ingredient in the maintenance of species. For example, Keddy and Reznicek (1984) have demonstrated that a large fraction of the native shoreline flora of the North American Great Lakes depends on fluctuating lake levels for the maintenance of appropriate habitat. There is interest to stabilize the water levels of the Great Lakes to facilitate the use of locks and docks. Even if hundreds of miles of shore line were set aside as nature reserves, with near constant water levels, a large fraction of the shore species would be lost because flooding disturbance is essential to the maintenance of habitat quality for these species.

Grime (1979) suggests an ecological classification of plants based on their differing abilities to tolerate stress or disturbance; species adapted to tolerate specific stresses or disturbances tend to occur in great variety in areas characterized by these stresses and disturbances, and in many cases are dependent on them for their continuance. No matter how large, a preserve will only include as permanent residents those species for which there are appropriate habitats, and that have somehow come to occupy them. In the case of many plant communities, especially those made up of long lived species adapted to persist by tolerating the specific stresses of their habitats, the dynamics of competition, exclusion, extinction, colonization, etc., essential to the concepts discussed above, play a role in determining species richness primarily by providing the stresses and disturbances that characterize the environment of the habitat for the species comprising the essential richness of the area. When dynamics are construed as a feature of the environment, the factors important to determine species richness in a reserve of long lived, stress tolerating vegetation are: inclusion of such individuals *in situ* in the reserve; endemism (an endemic may not have ever colonized an area, it may have evolved there); preservation of habitat (including water table, air and water quality and the natural variation of environmental conditions); and protection from mortality especially anthropogeneous. Such long lived, often endemic, plants with specific habitat requirements are among those most appropriately protected in reserves. Hodson (1989) attributes recent losses in the British Flora largely to the destruction of especially the older, less productive habitats of long lived stress tolerators. Some recent studies provide evidence that dynamic loss and gain processes are not very important in some vegetation when habitats are protected. Glass (1981) observes no species loss during the last century from some remnants of American prairie; and Game and Peterken (1981) report virtually no loss of forest understory herbs from centuries old reserves in Lincolnshire, some of which are only a few hectares.

Here, I discuss the concepts of preserve size and species richness, especially as it might apply to a vegetation of long lived stress tolerators, adapted to a specific habitat. I present a simple, static model of species participation in a vegetation of plants each

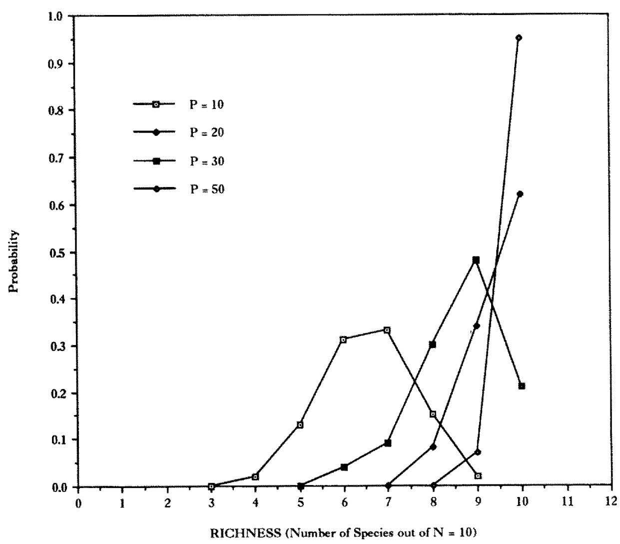

Fig. 1. Distributions for numbers of species from a pool of N = 10 for remnant sizes P = 10, 20, 30 and 50.

occupying roughly the same area, already established in a small remnant of their original habitat. The concepts also apply to one of two or more ecologically compatible and complementary groups (such as in a forest, the canopy and the floor; or in a fen, the hummocks and the wet runs between them) within which plants occupy roughly the same area. Suppose a small remnant of an original large area were preserved and its habitat protected. How many species would it have? The possible answers I will discuss here take the form of a probability distribution that says how likely each possible number of species would be. Subsequent questions can then be asked about the way these probability distributions change with changes in remnant size, and original species richness.

Methods

Richness probability distributions, which state how likely is each possible number of species in a given remnant, would depend on many things, including: the number of species in the original larger area; how evenly represented they were in that area; how much space each individual occupied; whether they occurred independently of each other in space, and how large a remnant was left. To get started, I will assume that the original species are all equally well represented, and that individuals of them occur independently in space and occupy about the same amount of space. These assumptions are most certainly not entirely true in nature, but they will enable us to deduce predictions in a straight forward way. We can then discuss how deviations from these assumptions might effect the predictions, especially regarding rare plants. I also assume that the habitat is full, and that the remnant is quite small in relation to the original area. I will not make assumptions about the number of original species, nor about the size of the remnant, but instead derive a variety of richness distributions, to discover the effects of remnant size and original richness.

Suppose that there were N species in the original vegetation (or in the subtype, e.g., canopy trees, fen hummocks, prairie clone clumps, etc.), and P places for individuals in the preserved remnant. Denote with g (R, P, N) the probability that there are exactly R species, from the possible N, among the P places for individuals in the remnant. The notation, g (R, P, N), represents symbolically the probability distribution that we seek. To be useful, we must be able to calculate the probabilities g (R, P, N) for specific numerical values of R, P, and N.

Suppose the size of the remnant were increased by one place; it has now P+1 places. The richness, R, might have increased by one if an individual from a species not formerly represented in the remnant were to occupy the new place. The richness would remain the same if the new space were occupied by an individual of a species already represented among the former P individuals of the remnant. We use the assumptions that the species are evenly represented and occur independently to calculate probabilities for each of these two possibilities. The richness would have increased by one, from R-1 to R, with probability

$$\frac{N-(R-1)}{N}$$

or remained the same, R, with probability $\frac{R}{N}$. Therefore,

$$g\,(R,\ P+1,\ N)=g\,(R,\ P,\ N)^{*}\frac{R}{N}+g\,(R-1,\ P,\ N)^{*}\frac{N-(R-1)}{N}.$$

This is a recursive relationship; it enables us to calculate subsequent values from previous ones. We know that

$$g\,(1,\ 1,\ N)=1.0$$

because if we have one space, we have one species.

$$g\,(1,\ 2,\ N)=N^{-1}$$

because the second place has a one in N chance of holding an individual of the same species as the first. In general,

$$g\,(1,\ P,\ N)=N^{-P+1}$$

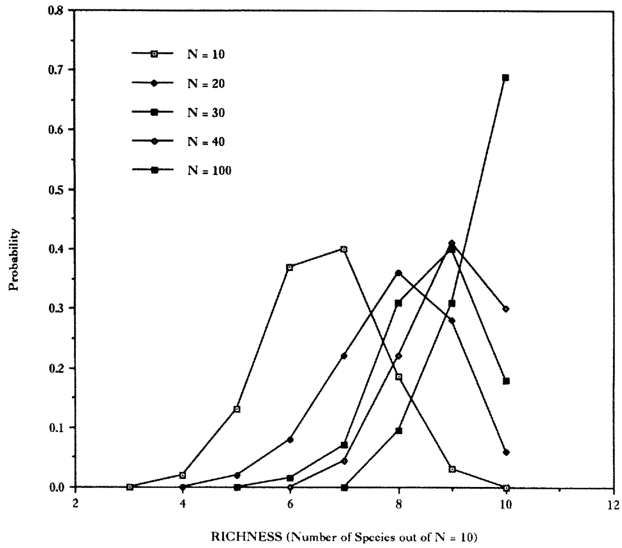

Fig. 2. Distributions for numbers of species for a remnant of size P = 10 and species pools N = 10, 20, 30, 40 and 100.

Now, for any N, we can start with a remnant of size one, and "grow" it with the recursion to any desired size. Using a computer, richness probability distributions were calculated for values of N up to 100, and for remnant sizes up to 300.

Results

Of the 30,000 probability distributions calculated, approximately 3,000 were printed (for even values of N and remnant sizes in multiples of 5 places). An example of a probability distribution for N = 20 original species and a remnant with room for 50 individuals would be:

of species	<15	15	16	17	18	19	20
Probability of that number	0	.005	.035	.136	.305	.355	.164

It would be very unusual for less than 15 species to be represented. About two thirds of the time there would be 18 or 19 species present. About one sixth of the time all species would be present.

It would be very inefficient to discuss these probability distributions individually. Inferences drawn from them are summarized in various ways in the figures. Figure 1 shows the effect of increasing remnant size for ten species of interest. A remnant with five times as many places as species is already very likely to contain all or nearly all of them. Figure 2 shows the effect, on richness in a small remnant, of N, the original species pool size. Figure 3 shows the effect of remnant size when N, the original pool size, is larger. Except for scale factors, it seems very similar to Figure 1.

This raises specific questions of how large must a

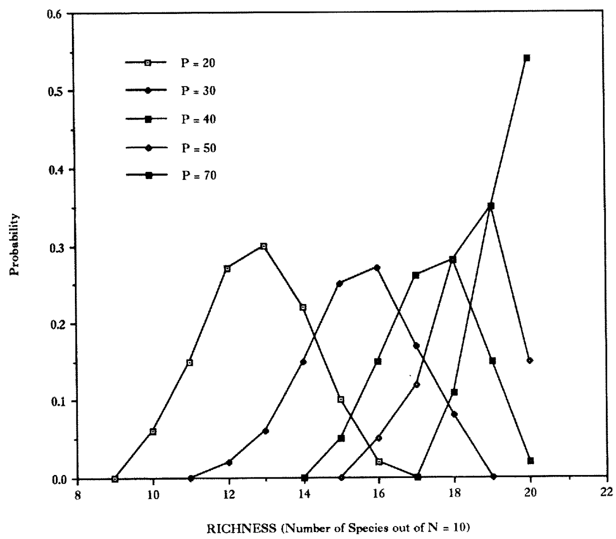

Fig. 3. Distributions for numbers of species from a pool of size N = 20 and remnant sizes P = 20, 30, 40, 50 and 70.

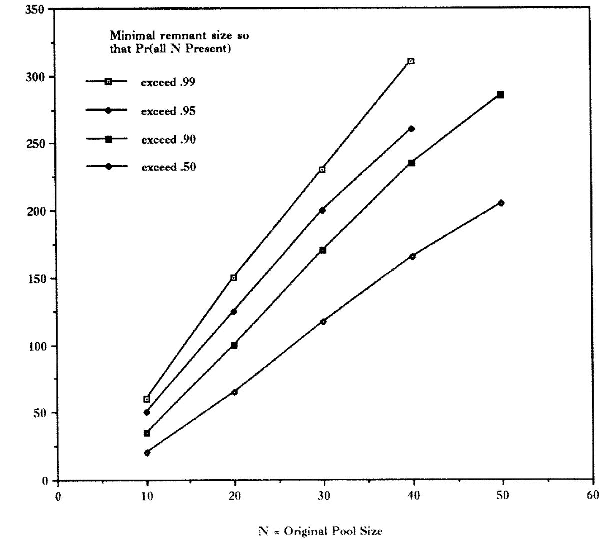

Fig. 4. Minimal remnant size P so that the probability that all N original species are present exceeds various thresholds.

remnant be in order to contain all (or at least a set fraction) the N species with a given (high) probability. Figure 4 presents remnant sizes, in units of numbers of individual plants, required to give various probabilities that all N species were present. Clearly, the higher the probability the larger must be the remnant, for a given original pool size. An area large enough for it to be 0.9 probable to have all species need be enlarged only about one seventh again to raise that probability to 0.95; but to raise it to 0.99 it would to be enlarged nearly half again. Figure 5 shows the same

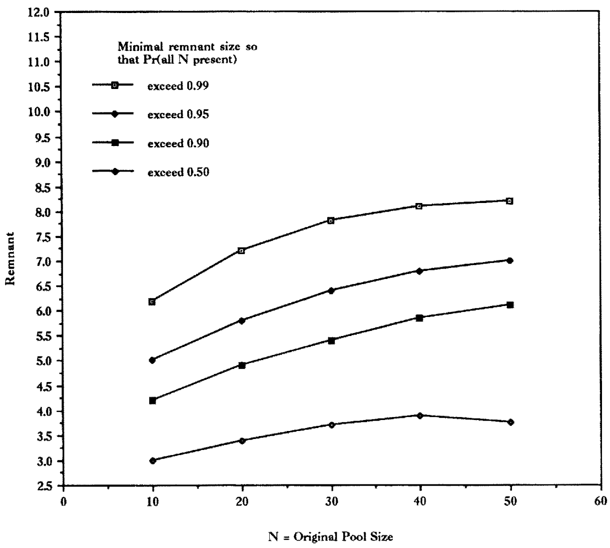

Fig. 5. Minimum remnant size so that the probability that all N original species are present exceeds various thresholds, divided by N.

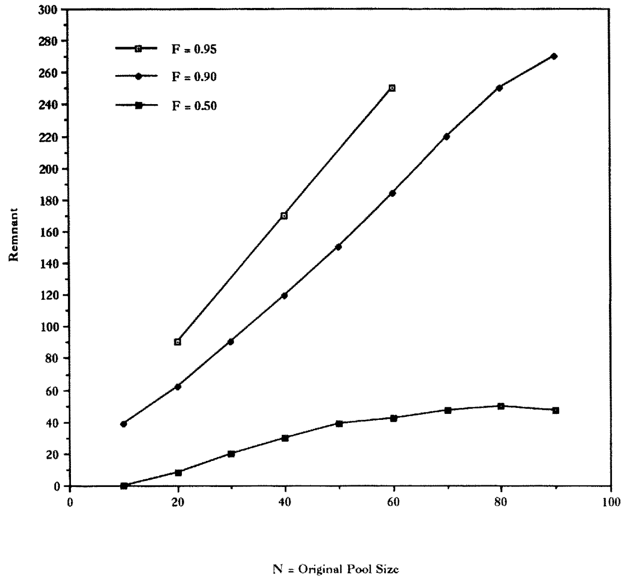

Fig. 6. Minimum remnant size P so that the probability that at least a fraction F of the N original species are present exceeds 0.99. Remnant sizes are plotted for three values of the fraction, F.

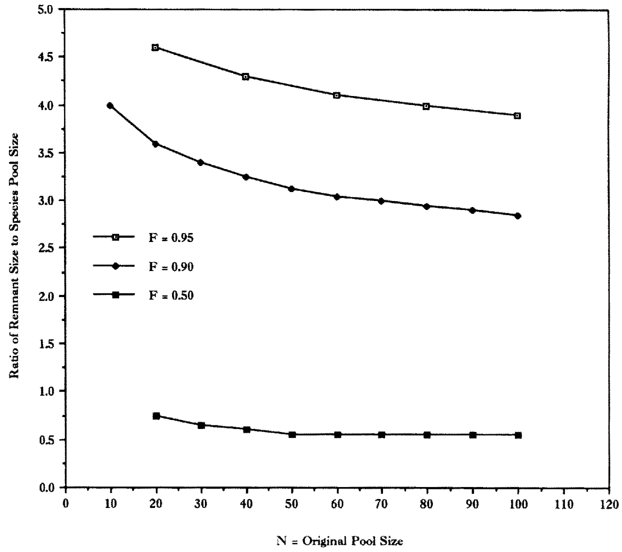

Fig. 7. Minimum remnant size P so that the probability that at least a fraction F of the N original species are present exceeds 0.99 all divided by N, the original pool size. Quotients are plotted for three values of F.

result, except there it is expressed in terms of the original pool size. As pool size becomes larger it requires a disproportionately larger (upward sloping curves) remnant to be equally likely to have all species represented.

Instead of requiring all the original species be present, we might be interested in the less stringent requirement that at least a given (high) fraction of them be in the remnant with very high (0.99) probability. These results are shown in Figure 6 for at least 0.5, 0.9, and 0.95 of the original N species present with probability 0.99. For small original species pools, these remnant sizes are only slightly smaller than those for all species to be present, but as original pool sizes increase remnant sizes may become substantially smaller to guarantee with high probability (0.99) that nearly (0.9 or 0.95) all of the species are present. In Figure 7, where these results are expressed in units of original pool size, (remnant size)/(pool size) quotients are seen to change very slowly for pool sizes over 30, with remnant sizes of 6 to 8 times the original pool size being adequate to include virtually all the species.

Discussion

Probability distributions to describe the number R of species represented in a remnant, with P individuals, of an originally much larger area of vegetation with N species have been derived under the symplifying assumptions that individuals are roughly the same size, occur with roughly the same frequency, and are sampled "with replacement" (i.e., the remnant is very much smaller than the original area). The probability distributions that arise as a consequence of these assumptions were examined and suggested that remnant sizes with the number P of places for individuals exceeding ten times the number N of species in the original vegetation are very likely to be large enough to contain nearly all N species. For example, in a forest with 50 tree species, a remnant large enough to hold 500 trees would very likely have at least one individual of each species. Fifty tree species is a somewhat rich forest vegetation and 500 trees is a somewhat small forest preserve. A preserve of 2000 trees, which would be likely to represent most trees several times to anticipate some mortality, is still a somewhat small forest preserve. Clearly, under these assumptions, the minimum size of a nature preserve needed to ensure that the species in the original vegetation are represented is fairly small. How is this conclusion affected by deviations from these assumptions? What other factors beyond mere representation are important to insure the maintenance of species richness in a nature preserve?

Size of mature individuals varies greatly among species, and size of individuals varies greatly within a species throughout the establishment and growth phases of development. Large differences in size often mean large differences in how an individual interacts with its environment, and in what constitutes a "place" for an individual to grow. In using these probability concepts to think about the relationship between area size and species richness, it is best to consider at one time only species with adults of about the same size for primarily ecological and biological reasons. In considering a single vegetation, several simultaneous analyses of area and size should be made, one for each major size group (e.g., canopy trees, understory trees, bushes and shrubs, geophytic herbs, and therophytes). In this way different plant sizes should not pose a serious obstacle to the use of these probability distributions.

What constitutes a place is more than an area of ground equal in size to that occupied by an individual plant in the class being considered. Places must meet the ecological requirements of the plants that grow in them: plants of limestone do not have places on granite; dry land plants do not have places in wetlands; south slope plants may not have places on north slopes. In this way, a large original area may be a composite of different kinds of places, each kind requiring its own remnant size and richness analysis. The classical curves relating observed numbers of species to an enlarging area of observation may take their shape from the early inclusion of different kinds of places and the ever slower later inclusions of the last few species to be found in those places. To determine what constitutes a place requires a knowledgeable plant ecologist. The inclusion of several distinct kinds of places in a natural area preserve may require a larger preserve so to ensure that the number of places of each kind exceed the minimum required.

It is well known that some species are more common and other species are less common. The reasons for this are not well understood. Sometimes it is because the suitable places for some are more common than the suitable places for others. In these cases, consideration of kinds of place will resolve this problem. Otherwise less common species are less likely to be represented than the probability distributions would suggest. One approach to estimate probability distributions that might reflect inclusion of the less common species using N* equal to 1/F, where F is the fraction of the total numer of individuals represented by a less common species. This will have the effect of increasing the minimum preserve size. Perhaps a more pragmatic approach would be to find individuals of the less common species and choose areas to preserve that are known to contain them.

Individuals of a given species do not typically occur randomly dispersed within an area where they occur. More frequently, they show a clumped distribution, often a consequence of their demographic history. Unless the clump size were very much less than the reserve size itself, to include the same number of species this clumping factor would require a larger preserve than suggested by the probability distributions. When a species is extremely clumped, it raises the possibility of inhomogeneous habitat, in which case simultaneous but separate analyses, as discussed above, might be more appropriate.

The probability distributions derived and discussed here are concerned with the inclusion of species in nature preserves. Clearly, if species are not included in a nature preserve then they are not preserved there. Inclusion may be sufficient protection for the short term, and for long lived plants that propagate principally vegetatively the short term may be quite long. However, if a species is to be preserved for the longer term consideration must be made of population level phenomena such as reproduction, development, genetic drift. These topics are discussed in some detail by Soule (1987). We can make some consideration of how they might impinge on the size of preserves. Reproduction requires a large enough number of reproductive individuals to ensure compatible mating types and gametic encounter. Development is of particular concern when plants in the seedling and establishment phase require a qualitatively different kind of place than that required by the reproductive individual. Genetic preservation also requires larger effective population sizes. All of these considerations suggest larger and more heterogeneous contiguous nature preserves.

No matter how large or small, nor how many or few species are included, no nature preserve will function if the environmental conditions required by its resident species are not also preserved. These include air and water quality; water table; water timing and natural variation; water flow; thermal and radiation regimes; and defense from inappropriate disturbance or competition, such as Off Road Vehicles and invasion by foreign weedy species.

Until these factors are understood better, natural preserves will fail. Thus it seems prudent to preserve to the extent feasible any area, large or small; to preserve with it the requisite environmental conditions to the extent that we can tell what they are and control them; and to continue to study the reproductive ecology and demography of wild creatures in their natural habitat.

REFERENCES

CONNELL, J.H. and E. ORIAS. 1964. Ecological regulation of species diversity. *Am. Nat.* 98: 399-441.

GAME, M and G.F. PETERKEN. 1984. Nature reserve selection in central Lincolnshire woodlands. In *Area and Isolation* Inst. Terrestrial Ecology, Oxford.

GLASS, W.D. 1981. The importance of refuge size in preserving legumes, goldenrods, and milkweeds. M.S. Thesis. U. Illinois Chicago.

GRIME, J.P. 1978. *Plant Strategies and Vegetation Process* John Wiley and Sons, New York. 157-189.

HARPER, J.L. 1069. The role of predation in vegetational diversity. *Brookhaven Symposium Biology* 22: 48-62.

HODGSON, J.G. 1989. What is happening to the British flora? *Plants Today* January: 26-32.

HUSTON, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.

KEDDY, P.A. and A.A. REZNICEK. 1985. Vegetation dynamics, buried seeds, and water level fluctuations on the shorelines of the Great Lakes. *In* H.H. Prince and F.M. D'Istri eds, *Coastal Wetlands*. Lewis, Chelsea, Michigan.

MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princenton.

Margalef, R. 1069. Diversity and Stability. *Brookhaven Symposium Biology* 22: 25-37.

Simberloff, D. and N. Gotelli. 1983. Refuge design and ecological theory: lessons for prairie and forest conservation. In R. Brewer (ed.) *Proceedings of the Eighth North American Prairie Conference* Western Michigan University Press, Kalamazoo, MI.

Soule, M.E. 1987. Editor. *Viable Populations for Conservation*. Cambridge University Press 189 pp.

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