

# REFUGE DESIGN AND ECOLOGICAL THEORY: LESSONS FOR PRAIRIE AND FOREST CONSERVATION<sup>1</sup>



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## INTRODUCTION

We are far from experts on prairie vegetation, but we can summarize some contributions that academic biology—ecology, biogeography, population genetics, etc.—has attempted to make to conservation, assess their value, and comment on whether they may be useful in prairie conservation.

Most current academic interest in conservation stems from the observation that, in the face of increasing human population, habitats of all sorts are increasingly insularized (Burgess and Sharpe 1981). This is as true of prairie as it is of forest. Effects of this insularization can conveniently be divided into 2 classes: (1) ecological and (2) genetic. We will treat both, though far more has been written and far more information is available about ecological consequences of insularization than about genetic consequences.

## ECOLOGICAL AND BIOGEOGRAPHIC CONSIDERATIONS

### The Species-area Relationship

One of ecology's oldest generalizations is the "species-area relationship," that large areas or islands tend to have more species of organisms than do small ones (Connor and McCoy 1979). Prairie data (e.g., Fig. 1) clearly depict this tendency (Glass 1981). Here we plot species lists, kindly provided by William Glass, of goldenrods, milkweeds, and legumes in 56 prairie fragments of different sizes in Iowa and Minnesota. These prairies consisted of all unplowed patches on the terminal glacial moraine that contained big and little bluestem and were not grazed to the point that *Amorpha canescens* was absent. It is apparent that bigger prairies have more species of all 3 plant groups total, or of any 1 of them like goldenrods, than do smaller prairies, and the statistics of the regressions bear this out (Glass 1981). Consequently it appears that if 2 prairie fragments are identical in every way (e.g., habitat diversity, cost, etc.) except for area, the larger 1 would make the better refuge if the goal is to conserve as many species as possible.

At the outset we should qualify 2 aspects of this statement. First, it is far from clear that the usual conservation goal is to conserve the most species (Simberloff and Abele 1982). Academic ecologists take this goal as given (e.g., Cole 1981, p. 631), but to us it seems that conservationists at least as frequently articulate a very different aim—to conserve certain species of particular interest. A prairie fan, for example, might say to hell with *Solidago rigida* and *Asclepias*

*syriaca* and principles derived from their distributions—he/she cares only about genuine prairie plants like *S. riddellii* and *A. sullivantii*! Second, conservation can never be forever. Paleontology tells us that no species is immortal. For example, of all animal species that have ever existed, at least 99% are extinct (Moore et al. 1952), and even though the rate of extinction has vastly accelerated because of recent human activity (Simberloff 1982a), most extinctions were in the geologic past and were not anthropogenous. Environments change, chance catastrophes occur, evolution proceeds, and every species is doomed to extinction sooner or later. The best we conservationists can hope to achieve by enlightened management practices is to defer the inevitable extinction. So when we say that a larger refuge is better than an otherwise identical but smaller one, we mean that the rate of extinction in the community is slower or, for a single species, that the expected time to extinction is longer.

### Island Biogeographic Theory and the One-Large-vs.-Many-Small Debate

Granted that a single large refuge is likely better than an otherwise equivalent single small refuge, a major controversy has recently arisen over a related question. Given a certain area (say 40 acres) to be set aside for conservation, is it better strategy for it to be deployed as several small refuges (say 4 of 10 acres each) or 1 large one? Again, one may ask (a) which configuration conserves the most species and (b) which is likely to defer the extinction of any particular species the longest. It is surprising that most authors have followed the lead of Wilson and Willis (1975) in espousing the single large refuge over the cluster of smaller ones for both goals (a) and (b), arguing that the equilibrium theory of island biogeography (MacArthur and Wilson 1967) provides theoretical justification for such a choice. The theory views the biota of an island (or insular habitat such as a refuge) as a dynamic equilibrium, with a more or less constant number of species maintained by a balance between local extinction of resident species and immigration of new ones. What is surprising about application of the island theory in this conservation context is that:

- (1) The theory itself has come under increasing criticism and has been shown to be at best an accurate depiction of only a few ecological communities (F. Gilbert 1980, Simberloff 1982b).
- (2) It was quickly demonstrated that the theory, whatever its merits in other settings, offers no prediction about whether 1 large or several small

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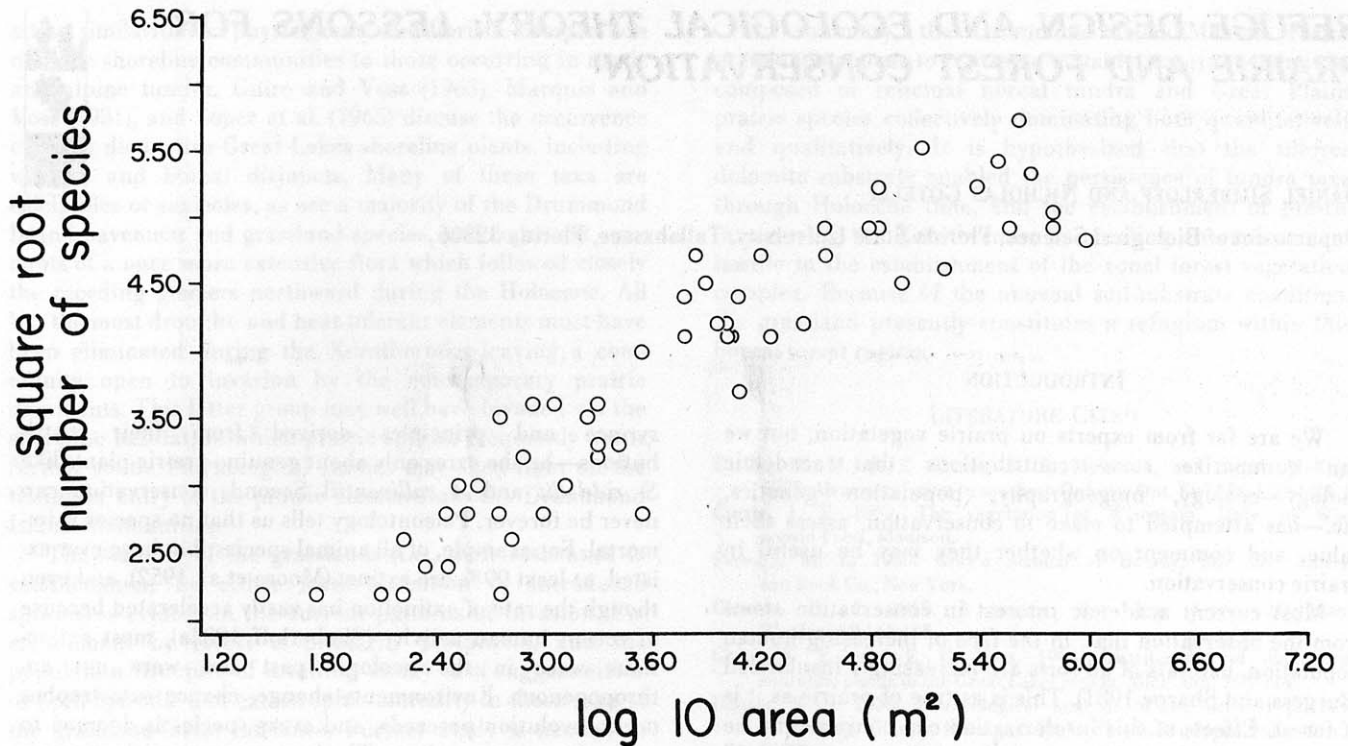


FIG. 1. Number of species of goldenrods, milkweeds, and legumes in 56 prairies studied by Glass (1981).

refuges is optimal (Simberloff and Abele 1976a, b, 1982; Higgs 1981).

- (3) The few published data relevant to the issue show that, for a variety of taxa, habitats, and regions, several small sites generally support as many species as 1 large site, or even more species (Simberloff 1982a, Simberloff and Abele 1982).

The reason why the pattern cited in (3) obtains—why several small sites usually have at least as many species as 1 big one, and often have more—is discussed below. For now we are interested in whether prairie plants adhere to this pattern. Using the Glass data on milkweeds, goldenrods, and legumes, we found that they do. We randomly lumped together samples of pairs of Glass's prairies, trios, quartets, and so on up to groups of 10 prairies. Each prairie was

TABLE 1. Six comparisons of species richness in single large prairies with that in groups of smaller ones, where total area is approximately equal. Data from Glass (1981).

SINGLE PRAIRIE		MULTIPLE PRAIRIES		
AREA (M <sup>2</sup> )	NUMBER OF SPECIES	NUMBER OF SPECIES	Σ AREA (M <sup>2</sup> )	NUMBER OF PATCHES
660	7	11	587	3
957	8	14	920	3
3,290	16	16	3,217	2
17,500	17	22	17,485	8
34,729	24	28	32,025	2
960,000	23	31	930,615	8

assigned a number, and numbers were then drawn randomly. None of these simulated groups exceeded in area the largest of the single prairies. For each group of prairies, we amassed a list of all species present in the group. If we now regress number of species on area for single prairies, then pairs, trios, etc., we find (Figs. 2 and 3) that for a given area, on average, there are slightly but significantly more species the more separate refuges comprise the area. With area the first independent variable, number of patches still contributes significantly to species richness ( $F = 45$ ,  $P < 0.001$ ). That is, prairie plants of these 3 groups seem to behave like a number of other taxa: at least over the size range of the prairies Glass studied, groups of small prairies have slightly more species than 1 larger prairie of equal total area. Table 1 lists several such comparisons. Glass (1981, Table 2) gives 2 other comparisons that tend in the same direction. We have no data on whether groups of smaller sites differ from single large ones in any way other than contiguity, but Glass (pers. comm.) feels there are no apparent consistent physical differences between his small and his large sites.

This may all be well and good, but if there are certain key species absolutely restricted to large prairies, we still might opt for single large refuges over groups of smaller ones. One way this question is typically addressed is by looking to see what is the minimum size of island occupied by each species (references in Simberloff and Abele 1982). Glass (1981) uses his data exactly this way to conclude that legumes and milkweeds can survive in even his smallest prairie (5.7 m<sup>2</sup>), but that goldenrods may have difficulty maintaining their populations in prairies smaller than 50 m<sup>2</sup>. We ordered Glass's 56 prairies from smallest to largest,

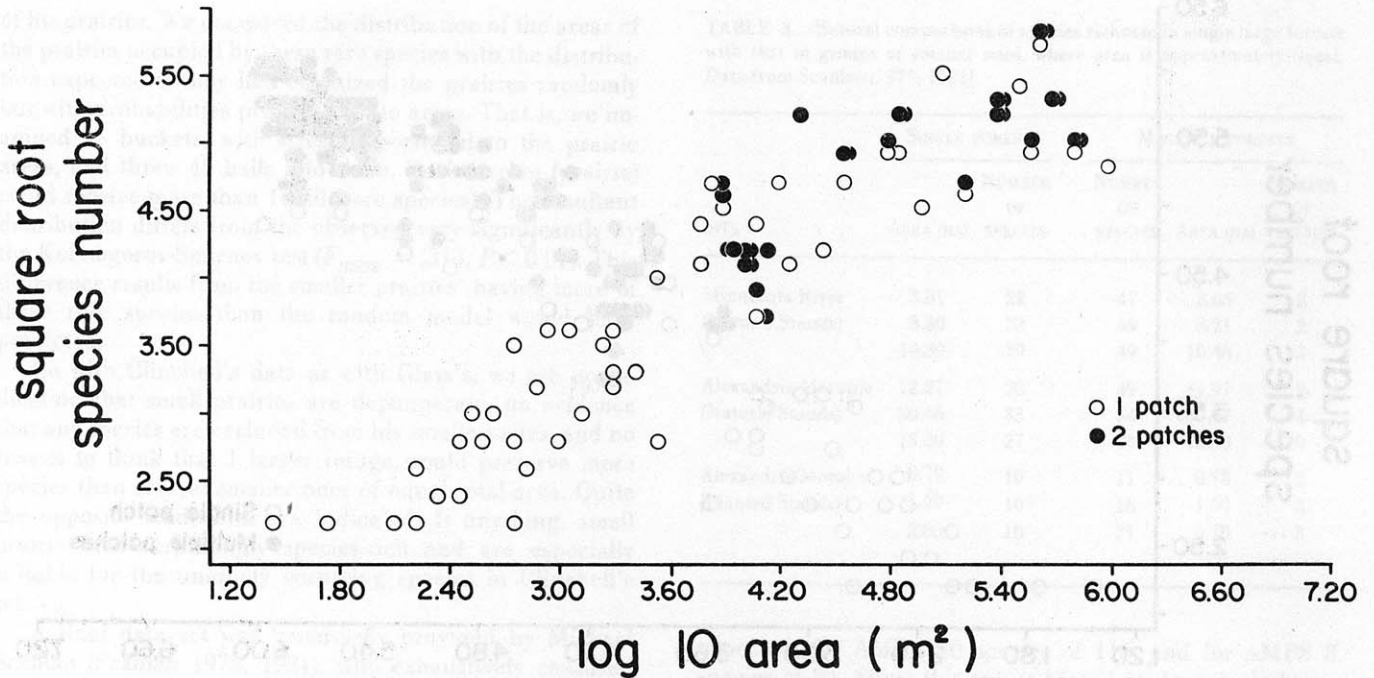


FIG. 2. Number of species of goldenrods, milkweeds, and legumes in single prairies and in groups composed of 2 randomly drawn prairies. Data from Glass (1981).

then for each of his 39 species found the rank  $L_i$  of the smallest prairie it inhabited. We then asked for each species  $i$ , if there were 56 buckets in a row (representing lowest rank on left and highest on right) and we randomly distributed its  $N_i$  occurrences among the 56 buckets, such that no 2 occurrences fall in the same bucket, what is the null probability that the left-most occurrence would have been even smaller than that observed ( $L_i$ ). This probability is

$$1 - \frac{\binom{56 - L_i + 1}{N_i}}{\binom{56}{N_i}}$$

and for 23 of the 39 species this probability is greater than 5%. That is, it appears that almost half the species are avoiding small prairies.

However, this minimum-inhabited-size approach neglects the species-area relationship. Since small prairies have fewer species, we would have expected rather few species in the smallest. It is as if the buckets are not of equal size, but rather the left-most ones are smaller and the size increases to the right. We constructed 2 models of random colonization that account for the species-area relationship. First, for Glass's data, we divided the prairies into 3 size classes: small = < 1,000 m<sup>2</sup>, intermediate = 1,000-12,000 m<sup>2</sup>, large = > 12,000 m<sup>2</sup>. We then asked, for each of his 39 plant species, how many of the prairies in each size class did it occupy? Of course smaller prairies have fewer species, as we pointed out above in discussing species-area curves. But a  $\chi^2$  contingency test showed that these species as a group do not "avoid" smaller prairies above and beyond the usual species-area effect. In fact, only 1 species, *Amorpha canescens*, of the 39 differs from the expected, given the marginal totals of how many species are found in each prairie and how many prairies each species occupies. That species tends to be found disproportionately in the smaller prairies.

Second, we constructed a mechanistic model of how a species  $i$  might come to occupy the sites that Glass observed, in order to examine the notion that at least some species "avoid" small prairies. We again considered 56 buckets, only this time they were different sizes, each bucket's size being proportional to the area of 1 of the prairies. For each species  $i$ , we simulated (by computer) throwing balls (representing propagules of the species) into the buckets until  $N_i$  of the buckets were occupied. That is, for every ball, the probability that it falls in bucket  $j$  is proportional to the size of bucket  $j$ . The  $N_i$  occupied buckets at the end of the simulation represent the occupied prairies. Having thus distributed each species' occurrences randomly among the appropriate number of prairies 10 times, we then compared, for each species, the observed areas of occupied prairies with the simulated expected areas by a Kolmogorov-Smirnov test. For only 1 species was there a significant difference ( $P < .05$ ) between observed and expected. By chance alone, even if no species were avoiding small prairies, we would have expected about 2 species ( $\approx .05 \times 39$ ) to show a significant difference. Once again we find no evidence that any species seem to avoid the small prairies.

Finally, we asked if Glass's small prairies tend to be depauperate in species. The model of the previous paragraph suggests not. To estimate the expected number of species  $E(S_j)$  for prairie  $j$ , we simply summed the simulated probabilities, over all species  $i$ , that prairie  $j$  contains species  $i$ . The variance for each species is the binomial variance, and the variance for each prairie is simply the sum of the variances over all species. When we compare  $S_j$  to  $E(S_j)$  we see that 25 of 56 prairies differ significantly from the expected species richness (14 > exp, 11 < exp), and the biggest differences are that a good fraction of the small prairies have more species than they should and that the large ones have fewer. All in all, for

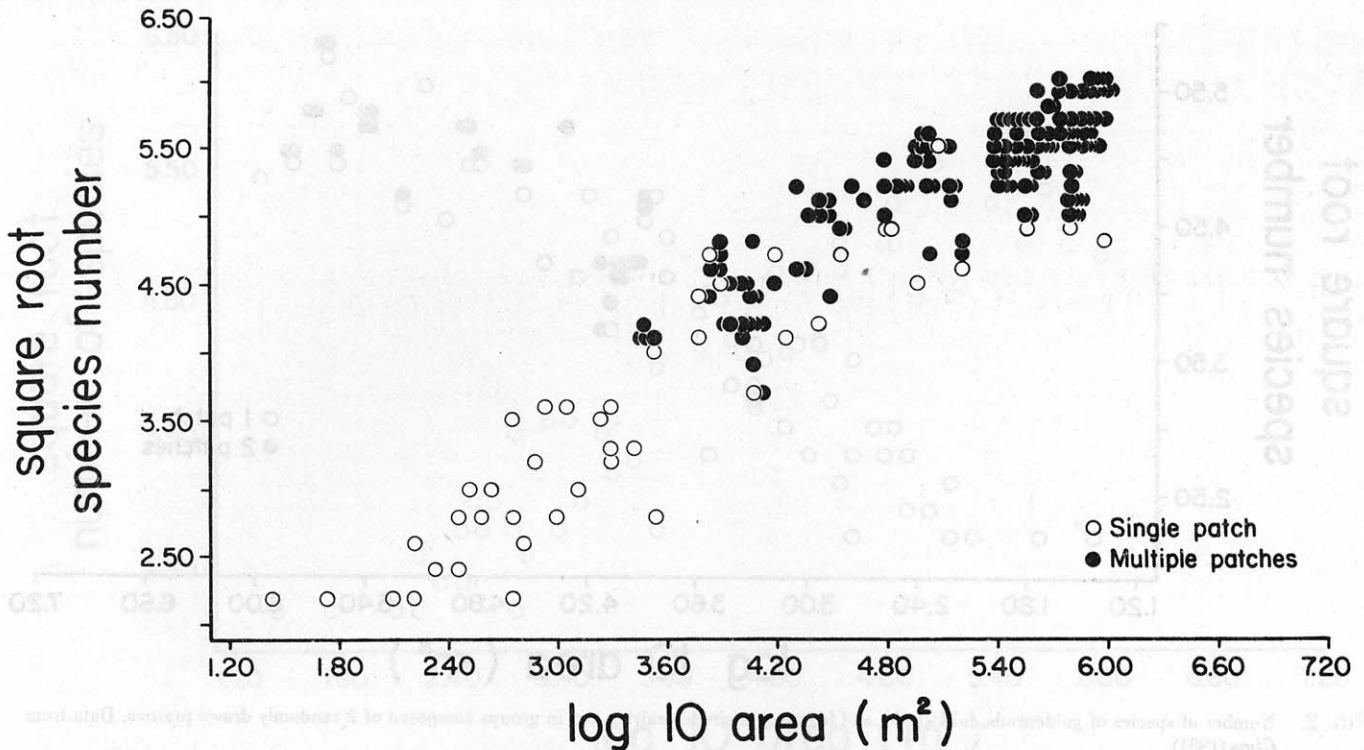


FIG. 3. Number of species of goldenrods, milkweeds, and legumes in single prairies and in groups composed of 2-10 randomly drawn prairies. Data from Glass (1981).

Glass's 3 plant groups, and over the size range of prairies he censused, there is absolutely no evidence that small prairies have surprisingly few species, that any species are excluded from small prairies, or that 1 larger prairie would be a better refuge than several small ones. If anything, the data show that a group of small prairies would likely contain more species than 1 large one, if total areas were equal.

A second data set, of all 152 angiosperm species on 15 prairies of varying size in Illinois, was kindly provided by Richard Clinebell, and allowed us to see whether the patterns we found for Glass's prairies obtain for a different data set. Once again (Fig. 4) there is a dominating species-area relationship ( $R^2 = .567$ ,  $P < .01$ ). As for Glass's data, we combined random sets of Clinebell's prairies (up to 5 prairies per set), and we found again that for a given area, on average, there are significantly more species the more separate prairies comprise the area. With area the first independent variable number of prairies still contributes significantly to species richness ( $F = 14.7$ ,  $P = .001$ ). In fact, for Clinebell's data, adding the number of prairies as a variable effects a major improvement in the regression, increasing  $R^2$  by .09.

Even using a model where prairie area is not taken into account (the row of equal-size buckets described above), we find only 5 of the 152 species have their smallest prairie larger than uniform random assignments would have predicted (see above description for formula). So there is no evidence that Clinebell's species avoid small prairies, even with a model biased to show that they do. When we randomly distribute the  $N_i$  occurrences of each species into prairies according to area (see model above—unequal buckets) we find that only 1 of the 152 observed occurrence patterns differed significantly by Kolmogorov-Smirnov test from the ex-

pected (derived by 10 simulations). The result is exactly as with Glass's plants. Finally, if we ask, as we did with the Iowa prairies, whether small Illinois prairies tend to be impoverished in species beyond what we would have expected from area alone, we find (see model above) that observed number of species,  $S_j$ , differs from its expectation  $E(S_j)$  in 9 of the 15 sites. The pattern of these differences is exactly as earlier: small prairies tend to have too many species and larger ones too few.

Finally, we analyzed a subset of Clinebell's plants separately. Of his 152 species, 45 are each found on only 1

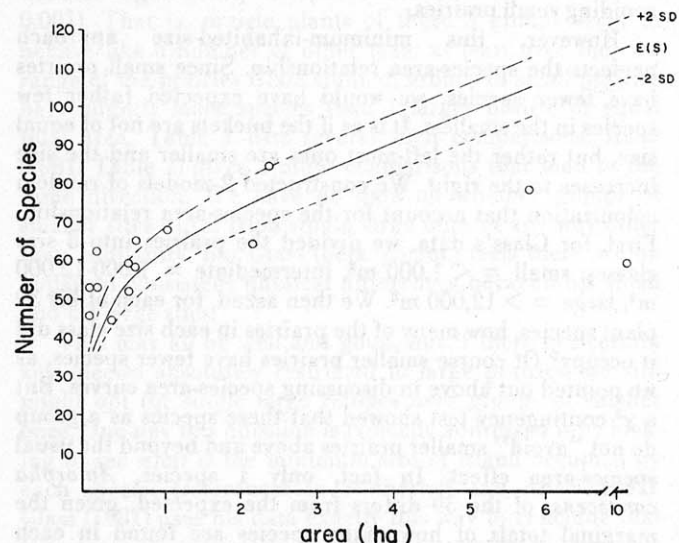


FIG. 4. Species-area curve for Illinois prairies studied by Clinebell, with best-fit curve and confidence limits (2 standard deviations from curve).

of his prairies. We compared the distribution of the areas of the prairies occupied by these rare species with the distribution expected if they had colonized the prairies randomly but with probabilities proportional to areas. That is, we imagined 15 buckets, with sizes proportional to the prairie areas, and threw 45 balls into them. Each bucket (prairie) could receive more than 1 ball (rare species). The resultant distribution differs from the observed very significantly by the Kolmogorov-Smirnov test ( $F_{max} = .313, P < 0.01$ ). This difference results from the smaller prairies' having more of these rare species than the random model would have predicted.

So with Clinebell's data as with Glass's, we see no indication that small prairies are depauperate, no evidence that any species are excluded from his smallest sites, and no reason to think that 1 larger refuge would preserve more species than several smaller ones of equal total area. Quite the opposite tendencies are indicated. If anything, small prairies are surprisingly species-rich and are especially suitable for the uniquely occurring species in Clinebell's set.

A final data set was generously provided by Michael Scanlan (Scanlan 1975, 1981), who exhaustively censused herbs in the understory of many forest patches embedded in the west-central Minnesota prairies. Of several such groups of forests that Scanlan examined, we treat 3 here:

- (1) The Minnesota River Tract (MRT)—12 remnants containing 102 species.
- (2) The Alexandria Moraine Natural Sites (AMNS)—22 remnants containing 116 species.
- (3) The Alexandria Moraine Planted Stands (AMPS)—43 planted forests containing 84 species.

All of Scanlan's groups adhere to the usual species-area relationships, and he also sought correlations between species richness and other variables, such as isolation (Scanlan, 1975, 1982).

We further subjected his data from the above 3 groups to the same sorts of analyses performed on Glass's and Clinebell's prairie data. First we combined random sets of forests (up to 4 for MRT, 10 for AMNS, and 5 for AMPS) to see whether 1 large or several small forests contained more species, on average. In all 3 groups, as with the Glass and Clinebell data, it was the latter. With area as the first independent variable, number of forests still increases species richness significantly (Table 2). Table 3 lists several specific comparisons for each group.

When we use the model of a row of equal buckets (area not taken into account) to see if species are excluded from small forests, we find for the MRT group only 1 of 102 species with a minimum forest size significantly larger than

TABLE 3. Several comparisons of species richness in single large forests with that in groups of smaller ones, where area is approximately equal. Data from Scanlan (1975, 1981).

SITE	SINGLE FOREST		MULTIPLE FORESTS		
	AREA (HA)	NUMBER OF SPECIES	NUMBER OF SPECIES	AREA (HA)	NUMBER OF PATCHES
Minnesota River (Natural Stands)	3.81	22	47	3.65	2
	8.30	32	49	8.21	2
	10.89	39	49	10.46	3
Alexandria Moraine (Natural Stands)	12.27	20	49	11.97	2
	30.66	33	54	30.67	4
	75.20	27	76	73.60	9
Alexandria Moraine (Planted Stands)	0.79	10	11	0.78	2
	1.60	10	18	1.60	3
	3.80	16	21	3.78	3

expected, for AMNS 10 species of 116, and for AMPS 8 species of 84. Since this test is biased as described above, we conclude that there is no evidence of exclusion from small forests. When we randomly distribute the  $N_i$  occurrences of each species into forests according to forest area (unequal bucket model), we find for the MRT group (10 simulations for expected) that none of the 102 species has a distribution of forest sizes significantly different ( $P < .05$ ) from expected, by the Kolmogorov-Smirnov test. For the AMNS and AMPS group (10 simulations each) we find only 2 species in the AMNS group differing at the 5% level from expected, but 7 such species in the AMPS group. We would have to find about 5 such species in each group (ca. 5%) to reject the hypothesis of random assignment. If we use the same model as we did for the Glass and Clinebell data to see if small forests are species-depauperate, we find exactly the same result: they tend, if anything, to have too many species given their area, while large forests tend to have too few. For the MRT group one finds the expected number of species differs significantly from that observed in 9 of 12 forests; for the AMNS forests the comparable figure is 14 of 22, and for the AMPS sites it is 19 of 43. For all 3 groups it is the small forests that are too speciose.

Finally, when we look at "rare" species (those found in only 1 forest) in all 3 forest groups exactly as we did for Clinebell's prairie plants, we find the same result (Table 4): a disproportionately large number of these species occur in small forests.

TABLE 2. Effect of number of islands on species richness for herbs of 3 groups of forests (data from Scanlan 1975, 1981).

FOREST GROUP	INCREASE IN R <sup>2</sup>	F	PR
MRT	.280	24.04	< .001
AMNS	.106	27.90	< .001
AMPS	.110	14.52	< .001

TABLE 4. Kolmogorov-Smirnov statistics for distribution of "rare" herbs in 3 groups of forests (data from Scanlan 1975, 1981).

FOREST GROUP	TOTAL SPECIES	"RARE" SPECIES	F <sub>MAX</sub>	P
MRT	102	36	.301	< .01
AMNS	116	31	.395	< .01
AMPS	84	36	.267	< .05

### Habitat Diversity

We thus see for data on 2 sets of prairie plants and 3 sets of forest herbs a recurrent pattern: no species are excluded from small refuges, and groups of small refuges tend to have a few more species than do single larger refuges of equal total area. This same tendency has been seen in a variety of other taxa (Simberloff 1982a). Among plants it has been noted by Game and Peterken (1981) for woodland herbs, Higgs and Usher (1980) for plants of Yorkshire limestone pavements, chalk quarry reserves, lowland heaths, and Scottish soft coastal habitats, Malyshev (1980) for plants of large regions, and Järvinen (1982) for woodland angiosperms in the Åland Islands. A likely explanation for this tendency resides in what is probably ecology's oldest and firmest generalization: each species is restricted to a range of habitats or microhabitats, and species differ in their optimal habitats. In fact, the most common explanation for the species-area relationship has traditionally been that larger areas have, on average, more habitats, and therefore have more species (Connor and McCoy 1979). Even though other forces may contribute to the increase in species richness with area (Simberloff 1976), habitat diversity must usually be the most important variable. It is reasonable to hypothesize, then, that on average a group of distinct refuges, simply by virtue of spatial separation, will encompass a greater variety of habitats than will a single refuge of equal total area. Game and Peterken (1981) propose exactly this explanation for their woodland herb results: a random collection of small woods would likely have more habitats than 1 large one would. They add that, if one set out to maximize habitat diversity, one could exaggerate the advantages of a group of small refuges by choosing diverse and unusual habitats. A similar conclusion was reached by Kitchener et al. (1980) for lizards of the Australian wheatbelt:

... while scattered small reserves, totalling  $1.78 \times 10^4$  ha, contain almost all known lizard species in the . . . wheatbelt, a single area . . . in order to contain the same number of species would need to be immensely larger—possibly by a factor of 600. This situation is again believed to reflect the heterogeneity of habitat within the region such that an enormous area is required to encompass all its habitat diversity and consequently to carry representatives of all lizard species in the region.

But there is a problem with our explanation of increased species richness on groups of small sites by virtue of increased habitat diversity: so far it is only a plausible story. In fact, even if all botanists would agree that each plant has species-specific habitat requirements, very rarely have these been precisely specified. Rabinowitz (1981) points out that many rare plants are rare because their required habitat is rare—*Solidago bartramiana* is an example. But for every plant that has been sufficiently studied to allow us to attribute rarity to habitat specificity there are dozens of rare plants where we are currently only guessing. In the prairie this situation obtains *a fortiori*, though precise explanations for rarity are beginning to appear for some species (e.g., Rabinowitz 1978, Rabinowitz and Rapp 1981). Platt (1975, Platt and Weis 1977, Werner and Platt 1976) has focused on differences between coexisting species, though he has been more concerned with what permits coexistence between species of similar habitat than with what habitat restrictions could make species rare or absent.

As a start in demonstrating the role of habitat diversity in maintaining prairie plant species diversity, we used a data set from the Konza Prairie supplied by L. Hulbert. Four hundred thirty-two 10-m<sup>2</sup> quadrats were exhaustively censused, to see not only which plants were present but how abundant they were (7 classes). Further, the soil type is known for each quadrat; there are 7 different types represented. Johnson and Simberloff (1974) and Game and Peterken (1981) have shown that number of different soil types correlates highly significantly with number of plant species over groups of sites, although it is not possible to say for these data whether the soils are directly determining which plants are where (Simberloff 1982c). There is also a literature showing that some plants are restricted to certain soils (references in Simberloff 1982c) but this also need not imply a strong role for soil type diversity in maintaining plant species diversity. For the Konza plants there were also various burning and mowing regimes and various periods and seasons for these disturbances. We know that such disturbances are critical habitat variables for many prairie plants (Hulbert 1969, Hover and Bragg 1981), perhaps as critical as soil type. But the records of disturbance are not yet available in computerized form, so we were able to treat only soil type.

For each of the 168 species, we found how many of the 432 quadrats it occupied. We then constructed, for each species, a  $7 \times 2 \chi^2$  contingency table, with rows as soil types and columns as presence or absence, to test whether the presences and absences in the quadrats of different soil type were independent of soil type. That is, does each species tend to be present in or absent from certain soil types disproportionately, given its total number of occurrences? The results are clear-cut: Only 36 species showed no significant deviation from expected given random occurrence in quadrats of different soil types. Four species showed significant deviations in the contingency table as a whole, but these could not be assigned to preference or avoidance of any particular soils. The remaining 128 species all deviated significantly from expected and the deviation resulted from extraordinary positive or negative association with 1 or more soil types. The data, in sum, support Hulbert's contention (pers. comm.) that a practised prairie worker could usually tell the type of soil in a quadrat from a list of the plants present. One must conclude, then, that to conserve a given species or set of them, one must have the appropriate soil. Surely a similar conclusion would arise from an analysis of other habitat data if these were available.

We also find for the Clinebell prairie data and Scanlan forest herb data that species that are rare (or at least have small geographic ranges in these regions; Rabinowitz (1981) discusses what is meant by a "rare" species) tend to be found more frequently in the smallest sites than one would have expected if species were assigned randomly to sites on the basis of areas. And larger sites tend to have too few of these "rare" species. Why this pattern exists we cannot guess, unless it is simply a manifestation of the tendency we found in all the data sets we examined for small sites to have too many species and larger sites to have too few relative to random expectations. That is, it may be that "rare" plants (rare in this sense, anyway) are not distributed differently according to site size than are other plants. In any event,

the conservation message is clear: this result reinforces our conclusion that groups of small refuges may be better than single larger ones. Järvinen (1982) also found that more "endangered" vascular plant species in the Åland Islands tend to be found in groups of small islands than on single large ones.

W. Platt (pers. comm.) has observed that the goldenrods, milkweeds, and legumes of Glass's (1981) study encompass a number of "weedy" species that are not "good" prairie plants and are especially suited to survival in small sites, and further that many of Glass's prairie sites exist today precisely because of their unusual habitats—stony or odd soil, severe slope, etc. Consequently he cautions that results from Glass's data might inordinately favor groups of small refuges and might not be valid for prairie plants as a whole. It is similarly true that Clinebell's small prairies include a number that likely have aberrant physical habitats, though Clinebell studied all species. Clinebell's and Scanlan's species lists do not include particularly large proportions of "weedy" species. Platt is correct to be cautious here, but at least Glass and Clinebell have data that can be brought to bear on conservation questions; even if the data sets are not the best ones conceivable for this purpose, they are the best there are. Although Platt's supposition that these sites may have aberrant habitats is reasonable, it is certainly not demonstrated. Nor, to our knowledge, have the exact habitat requirements of prairie plants been systematically determined, so we are not in a position at this time to discount lessons from the Glass and Clinebell studies.

That the prairie sites we have treated have unusual habitats may well exaggerate the expected increase in habitat diversity for groups of small sites compared to single large ones, although we have no data to test this. Similarly, that Glass's prairies are spread over such a large region means that our random subsets of them were especially likely to encompass substantial habitat diversity. In general, one might predict that the greater the distances among the small sites in a group, the larger the increase in number of species over that contained in a single, even large, site.

#### Insularization, Minimum Areas, and Species Loss

Much of the literature arguing against single small refuges or even groups of them (e.g., Terborgh 1974, Diamond 1975) stems from an observation plus a largely untested model that extends the observation. The observation is that, all other things being equal, an island usually has fewer species of any taxon than does an equal-sized quadrat on the mainland (MacArthur and Wilson 1967). One may always question whether 2 habitats are really equivalent, but if we take the observation at its face value, the standard explanation is that all species on the island must maintain their populations only on the island, while species in the quadrat may include several that are partially maintained in the surrounding matrix and only partially in the quadrat and others that are actually maintained in the surrounding matrix (say, because of a unique habitat there) and are only transients, albeit common ones, in the quadrat (MacArthur and Wilson 1967).

This explanation, in turn, is extended to imply that, when a hitherto continuous land mass is broken into pat-

ches or islands by either rising sea levels or anthropogenous destruction of vegetation, the islands will lose species and eventually come to a new, lower equilibrium. They do so because the same patch of land as an island can support fewer species than it does as a part of a larger contiguous land mass. The decline in species richness, though plausible, has to our knowledge been directly observed only once (Simberloff 1976), for insects on 3 very small mangrove islands, where a drop of ca. 12% to a new equilibrium was observed over 7 months. A second widely cited example, the avifauna of Barro Colorado Island (formed during the construction of the Panama Canal), is inappropriate since much of the island has undergone drastic habitat change since its formation (Simberloff and Abele 1976b). No other study records the number of species originally present on an island, but 3 authors (Diamond (1972) for New Guinea satellite island birds, Terborgh (1974, 1975) for West Indian birds, and Wilcox (1978) for reptiles of Gulf of California islands) have estimated numbers of species present before the late Pleistocene sea level rise and thus inferred the subsequent decline to present numbers. The estimates and/or courses of sea level rise are questionable in all 3 instances, however (Abele and Connor 1979, Faeth and Connor 1979). Fossil evidence can occasionally demonstrate an extinction, but cannot show whether species richness declined since it cannot indicate which species were originally present. Whitcomb et al. (1981) hypothesize a decline in avifaunal richness in eastern deciduous forest, but do not estimate how many species were originally present or document any actual local extinctions. On a larger scale, by World War II less than 1% of eastern virgin forest remained in the U.S., but this severe fragmentation has so far resulted in the extinction of at most 2 bird species, the Carolina parakeet and the ivory-billed woodpecker (Terborgh 1975). For his prairie plants, Glass (1981) concludes, on comparing species-area relations of isolated remnants with those of quadrats in larger prairies, that no species number decline has occurred, and some of his remnants are a century old. Game and Peterken (1981) use the same method on herbs of Lincolnshire forests, some of which are centuries old, and reach the same conclusion: even in woods of just a few hectares, species loss, if it occurs at all, is extremely slow.

So it is far from clear that a decline in species number automatically follows habitat insularization or that, even if there is a decline, its magnitude and speed are sufficient to warrant conservationists' attention. An assessment must be made anew for each biota, with 2 questions in mind:

- 1) At the areas we are actually dealing with, what is the approximate rate of any potential species number decline?
- 2) Is there some "critical area," below which extinction rates are greatly increased and above which they are quite low and not strongly related to area?

Shaffer (1981) has recently summarized evidence for a minimum viable population size. If one assumes a constant average density, this translates into a minimum refuge area. This minimum is determined by a population's need to respond to 4 sorts of random or stochastic events. First is demographic stochasticity—chance aspects of the survival and reproduction of small numbers of individuals. For example, the likelihood that all offspring in some generation

will be male is greatly increased in small populations. Second is environmental stochasticity, the usual range of variation in habitat parameters and sizes of interacting species (like predators) that any population faces. Simberloff (1982a) gives examples of how small populations are especially vulnerable to effects of such variation. Third is the occasional occurrence of natural catastrophes like fires and floods, which also wreak greater havoc on smaller populations. Fourth is genetic stochasticity, discussed below, which is more severe the smaller the population.

MacArthur and Wilson (1967) and Richter-Dyn and Goel (1972) provide theoretical models in which extinction from demographic stochasticity is non-linear, with a critical size above which extinction is unlikely. The birth and death rates that are the parameters of these models are unknown for any organism, including prairie plants. There are several reasons for thinking that for plants in general, and many prairie plants in particular, these critical population sizes, if they exist at all, may be very small indeed, and the expected time to extinction usually very long (and, consequently, the rate of species loss very low).

First, many plants are extremely long-lived, either as individuals, such as some trees, or as clones or genets containing many vegetatively produced identical ramets, as in species of *Solidago* and other herbs (and also trees, such as aspen). Harper (1977) observes that a clonally reproducing herb or shrub is genetically equivalent to a large tree lying on its side, and there is evidence for some plants that individual clones may be as old as the most longevous trees. Oinonen (1967a, b, c) has found bracken and ground pine clones of nearly half a mile diameter, weighing many tons, and perhaps 1,500 years old. Similar observations abound for other plants (references in Harberd 1961). Harberd (1961) found in 1 small Scottish population of the fescue *Festuca rubra* very few clones, mostly large and apparently very old. He concludes that this population is not in delicate equilibrium with its environment and is not composed of precarious clones about to be outcompeted by genetically superior ones when such arrive. In fact, new seedlings, even if far superior genetically, would have almost no chance of survival against the well-established, vegetatively maintained existing clones. Mortality of established clones is very low, and any change in genetic composition of the population is exceedingly slow, taking centuries at least. The same conclusions could almost as well be drawn for whether *Festuca* would be replaced by other species, barring major habitat change, and this population comprises an area as small as the smallest of Clinebell's and Glass's prairies.

For *Trifolium repens*, a clover, Harberd (1963) finds more clones and smaller ones, but still fewer clones than ramets, and feels many of these clones are very old. For the grass *Holcus mollis*, there are very few clones in a large population, and each clone seems to span a variety of microhabitats (Harberd 1966). Some are over half a mile across and must be ancient. On the other hand, Harberd and Owen (1968) found in a different population of *Festuca rubra* than the above one that there were many more clones, mostly quite small, while Cahn and Harper (1976) found a similar result in a different population of *Trifolium repens* than that studied by Harberd (1963). It could be that some frequent ecological disturbance, like grazing (Cahn and Harper 1976) or fire (Oinonen 1967a), promotes seedling

establishment and thus speeds up the process of genotypic change or species replacement, while in the absence of frequent disturbance such processes are vastly slower than animal ecologists envision.

For prairie plants we know of no data comparable to the above, though many prairie plants are perennial and reproduce vegetatively. Platt (pers. comm.) feels that at least some prairie *Solidago* species consist of very long-lived clones, but many more data are needed. It is likely, however, that at least for prairie perennials any species number decline after insularization will be very slow, at least in the absence of major internal habitat change, unless the islands are minuscule—say, a few square yards. With long-lived plants, a small population is not automatically endangered if its habitat is protected (Rabinowitz 1981). The legendary Ashe's birch (*Betula uber*) apparently persists in a population of only 13 trees and 21 seedlings, and has been as rare as this for nearly a century (Ogle and Mazzeo 1976). If its habitat is protected, there is little reason to think it cannot persist for millennia. Rabinowitz and Rapp (1981) have even shown how certain tallgrass prairie plants that are favored in no habitat and are thus rare wherever found are nonetheless evolutionarily adapted to rarity and are not endangered so long as tallgrass prairie persists in their geographic ranges. On a larger scale, Simpson (1974) suggests that most of the decline in plant species richness in the Galápagos archipelago from the period of maximum Pleistocene areas (peak glaciation) has yet to occur. And Diamond (1972) and Terborgh (1974), for birds, similarly envision the decline as requiring millennia. Again, neither Simpson's study nor those on the avifaunas have direct evidence of how many species were originally present, so there is no proof that a decline occurred.

#### GENETIC AND OTHER CONSIDERATIONS

Genetic considerations are often said to mandate both very large population sizes and single large refuges rather than several smaller ones of equal total area. Frankel and Soule (1981) present the most strident exposition of this view. Small populations are a genetic anathema to Frankel and Soule for 2 reasons:

- (1) In the short term, inbreeding depression will lead to lower fitness; both survival and reproduction will decrease.
- (2) In the long term, the loss of genes resulting from genetic drift will lessen the ability of species to respond evolutionarily to environmental change.

There is no doubt that inbreeding depression is often a very serious matter for small populations of animals, through both the increase in frequency of homozygous recessive major defects and the less obvious but nonetheless real decrease in general fitness that often accompanies the decreasing heterozygosity imposed by inbreeding. Ralls et al. (1979) provide good evidence for the latter effect in several ungulate species, while Brückner (1978) shows inbreeding depression in morphological, physiological, and behavioral traits in honeybees. For plants the evidence is more ambiguous. On the 1 hand, many plants are predominantly selfers, and a study of 4 such species (Brown 1978) shows apparently healthy, persistent populations of each with absolutely no heterozygosity at all. On the other



hand, 2 of the species (*Oenothera biennis* and *Avena barbata*) had individual populations that were approximately 50% heterozygous. On average, these 4 species had quite low heterozygosity, and for none of them is there direct evidence that heterozygotes are superior. It appears (e.g., Clegg et al. 1972, Allard 1975, Kahler et al. 1975) that the strongest selective pressure on breeding system in at least 2 of these species is to facilitate preservation of certain multilocus combinations, rather than to optimize degree of heterozygosity per se.

Schaal and Levin (1976) found for the obligately outcrossing perennial prairie herb *Liatris cylindracea* that survivorship, reproductive output, and vegetative production are all greater in more heterozygous individuals, and age of reproductive maturity is lower. Similar results are known for about 10 other plants (reviewed by Schaal and Levin 1976). Of course the fact that genotype *A* will be selected over genotype *B* within a population need not imply that a population of all *A*'s will persist longer than a population of all *B*'s (e.g., Hamilton 1971). This fact plus the existence of homozygous populations blithely persisting apparently indefinitely (previous paragraph) in spite of their genetic homogeneity suggest that inbreeding depression in plants may be less important than the ecological dangers of small population size.

We are skeptical, especially for prairie plants, about the threat that loss of genes by drift in small populations poses to the ability of species to evolve in response to environmental change. Franklin (1980) and Frankel and Soulé (1981) suggest that an effective population size of 500 is required to maintain this ability, while Berry (1971) feels that there is so much genetic variation even in small populations that drift is unlikely to depauperate the gene pool significantly. Further, he notes that, "Observed selection pressures are so strong that any limitations on population size due to a reserve of finite size becoming an ecological isolate, are extremely unlikely to produce random and possibly deleterious genetical changes due to drift."

Whatever the minimum number of individuals a species needs in order to retain sufficient evolutionary potential, whether these should be maintained in 1 large or several smaller sites is, on genetic grounds alone, far from certain. Frankel and Soulé (1981), concerned with the dangers of inbreeding depression, opt for the former arrangement. By contrast, Drury (1974) and Chesser et al. (1980) recommend several small subpopulations. The genetic advantage they see in this strategy is the maintenance of different genes in the different populations, both by chance and by different selective regimes. Inbreeding depression within the subpopulations can be countered by deliberate occasional cross-breeding, but not so much as to obliterate genetic differences between the subpopulations. With prairie plants, for example, one could transplant individuals (or ramets) occasionally or hand-pollinate. The sizes of the subpopulations can, according to Chesser et al. (1980), be very small indeed without major inbreeding depression problems so long as there are occasional migrants. They recommend for 100 deer, for example, starting with 10 refuges of 10 individuals each and maintaining about 20% outbreeding.

Drury (1974), Simberloff and Abele (1976a), Chesser et al. (1980), and others all recognize that the effects of potential catastrophes such as fires, contagious diseases, and

storms would be less severe in several small refuges than in 1 large one. Even Frankel and Soulé (1981) concede this point. Drury (1974) and Simberloff (1982b) give examples from the animal literature of the threat to species consisting of 1 population. Surely the same principle applies to plants. Can one doubt that Ashe's birch would be safer were its individuals in 2 widely separated populations of 17 trees each than it is with a single population of 34?

Finally, there may be differences between single large refuges and groups of small ones in management cost and efficacy. Economies of scale would seem to lessen cost for single large refuges (Simberloff and Abele 1982), while Higgs (1981) observes that a single reserve may, on average, reduce detrimental outside influences. For example, control of an entire catchment area makes it easier to control water quality. Similarly, Hirsh (pers. comm.) observes that, if prairies are sufficiently small, their management (e.g., controlled periodic burning) is a nightmare. So at some size, management considerations alone dictate a halt to further subdivision of refuges, just as do biological considerations (see below). On the other hand, there may be increased pressure to "nibble away" at single large reserves just because they are large and so seem able to withstand small inroads of "development" (Higgs 1981). The end of such a process could well be death from a thousand cuts. Helliwell (1976) shows for vascular plants of 106 woods in west Shropshire that small isolated woods are not species-depauperate, and feels that their floras are more "valuable" in a conservation sense (by virtue of the numbers and rarity of their species). He sees the cause for this in the tendency for larger woods to be more intensively managed for timber.

#### SUGGESTIONS FOR PRAIRIE REFUGES

Two overriding points are clear from our analysis of the prairie plant data and consideration of the genetic, ecological, and conservation literature:

- (1) The key requirement for conservation of any prairie plant, or for communities of them, is the establishment of refuges with appropriate habitat.
- (2) There is no justification for assuming that single large refuges are automatically the best strategy, though in all circumstances maximum *total area* is probably desirable.

We have throughout said nothing whatever about aesthetic considerations, and do not feel ourselves particularly qualified to do so. It is obvious to us that there is an indescribable aesthetic and even spiritual pleasure that derives from standing in the middle of an enormous prairie such as the Konza, with no intervening habitat breaking the sweep of our vision. No cluster of small prairies will provide this feeling, and for this reason alone it seems imperative to set aside some very large tracts. But we have addressed conservation of biotic diversity, not aesthetic vistas, and it is important to separate these 2 goals. For the first goal alone, enormous refuges need not necessarily constitute the optimal disposition of available money. No amount of ecological research can address the second goal; it is a matter for neurophysiologists and artists.

The above 2 conclusions, however, actually constitute a call for an enormous amount of detailed field research if

one is to establish effective refuges. First is all the autecology that goes into finding out exactly what *are* the habitat requirements for the species of interest and the biological idiosyncrasies that make intensive research interesting. Second, even if the above evidence points to several smaller rather than 1 larger refuge as a possible strategy, at some point the individual refuges become so small that extinction rates within them are vastly increased (Simberloff and Abele 1976a), and we want to learn some indication of just what that size is, perhaps by monitoring over time the smallest of Clinebell's and Glass's prairie islands to see how frequent local extinction is. For reasons stated above, such extinction may not be a major problem in any time scale we will worry about for prairie plants even in very small sites, but it would be nice to have data to support this guess. Third, Pickett and Thompson (1978), Foster (1980), L. Gilbert (1980), and Grubb et al. (1982), among others, have all emphasized that many species require various forms of occasional disturbance, such as fire, for their continued existence. Platt (1975) has demonstrated this requirement for a number of prairie plants. Hover and Bragg (1981) note the importance of maintaining a variety of disturbance regimes for conservation of prairie plants, and Opler (1981) reaches similar conclusions for prairie insects. Consequently, whatever arrangement of refuges we settle on, we must ensure that some fraction of them are subjected to the sort of disturbance that will maintain plants of all successional stages. Because prairie succession is relatively rapid, it should be quite feasible to maintain areas at all seral stages simultaneously. Fourth, when species are demonstrated to be so rare that inbreeding depression may rear its ugly head, we should give careful consideration to several emergency measures, such as transplanting and hand-pollination. But such measures ought to be used only *in extremis*, as we know that some completely homozygous plant populations are very viable, rarity *per se* does not mean extinction is imminent, and genetic adaptation to local conditions will be hindered by cross-breeding. Much research is required on all these genetic aspects of prairie plants.

This sounds like a tall order indeed. In a seminal paper on plant communities, Watts (1947) suggested an analogy to T. S. Eliot's admonition to those who would study Shakespeare: "We must know all of it in order to know any of it." Certainly a plant community is a complicated entity, but ecology has come a long way since Watt's pessimistic dictum. In particular, the holistic view of plant communities that so dominated ecology when Watt wrote has been challenged, with the revolution beginning in exactly the same year—1947 (Simberloff 1980). A plethora of population-oriented research has demonstrated that progress in understanding the structure and function of communities is accessible through the analytic approach that has served the chemical and physical sciences so well. We do *not* have to know all about a community to know anything about it, and we are very likely to learn quite a bit about how to conserve communities if we accelerate the sorts of studies outlined above on key species or small groups of species. Throughout, we should beware of the global generality, particularly when it rests on theory or on data from species very different from those that concern us. The small prairie and forest relicts that are apparently

suitable for herbs might well lack characteristic mammals, birds, and even insects. Similarly, even if it should turn out that several small prairies typically contain more animal species than single large ones, "small" for animals may be a good bit larger than for plants. Only direct study will address such matters.

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