Effects of Insularisation on Plant Species Richness in the Prairie-Forest Ecotone

Daniel Simberloff & Nicholas Gotelli

Department of Biological Science, Florida State University,
Tallahassee, Florida 32306, USA

ABSTRACT

Data on plants from five groups of remnant prairies and forests in the prairie-forest ecotone of the midwestern United States show that: (1) Archipelagos of small sites tend to contain more species than do single large ones of equal total area. (2) No species are excluded from small sites. (3) Small sites tend to have surprisingly many species, and large sites surprisingly few, relative to a random colonisation model. (4) 'Rare' species (those that occur in only one site) are found more often in small sites than a random colonisation model would predict. (5) There is no evidence for any of these sites that species number is 'relaxing', but all these sites have been remnants for only a short time. Result (1) is consistent with results from similar studies on other taxa and suggests that there is no automatic reason to believe that species richness is maximised by single large refuges.

INTRODUCTION

Habitat insularisation (Burgess & Sharpe, 1981) is perhaps nowhere more pronounced than in the prairie-forest ecotone of the midwestern United States. Even before man's interference the ecotone was not a smooth border, but contained small prairie islands isolated in forest and small forest islands embedded in prairie. In the last 150 years urbanisation, agriculture, and silviculture have accelerated this insularisation. As virgin prairie and first-growth forest continue to decrease in extent, we wish to consider what sorts of fragments, among those remaining, would be likely

27

to conserve the most herb and shrub species. Specifically, we ask two questions. First, is species richness greater in a single large refuge or in an archipelago of small ones, where total area of the archipelago equals area of the large refuge? Second, how are individual species distributed among remnants of different sizes? To this end we examine five data sets:

(1)   The 39 goldenrod *Solidago*, milkweed *Asclepias*, and legume species of 56 prairie remnants in Iowa and Minnesota (Glass, 1981).

(2)   The 152 herb and shrub species of 15 prairie remnants in Illinois (R. Clinebell, pers. comm.).

(3)   The 102 understorey herb species of 12 natural forest remnants in the Minnesota River Tract, Minnesota (Scanlan, 1975, 1981, pers. comm.).

(4)   The 116 understorey herb species of 22 natural forest remnants in the Alexandria Moraine, Minnesota (Scanlan, 1975, 1981, pers. comm.).

(5)   The 84 understorey herb species of 43 small planted forests in the Alexandria Moraine, Minnesota (Scanlan, 1975, 1981, pers. comm.).

There may be a host of differences between single large and groups of small refuges in management cost and efficacy that we do not touch on here. Higgs (1981) and Simberloff & Abele (1982) mention several of these. For plants in general (Pickett & Thompson, 1978; Foster, 1980; Grubb *et al.*, 1982) and prairie plants in particular (Hover & Bragg, 1981) many species require periodic disturbances of various sorts, like fire. If the components of an archipelago of small sites are too small, such planned disturbance would probably be very difficult (Higgs, 1981; D. Hirsh, pers. comm.). On the other hand, there may be increased pressure to 'develop' parts of single large refuges just because they seem large enough to be able to sustain such inroads (Higgs, 1981). We have not treated any of these matters, nor have we addressed aesthetic considerations.

BIOGEOGRAPHICAL PATTERNS

Species–area relationships

The 'species–area relationship', that large areas or islands tend, *ceteris paribus*, to have more species than do small ones, is one of ecology's oldest

TABLE 1

Species–Area Statistics and Minimum Site Size (ha) for Two Data Sets
discussed in Text. All Probabilities are less than 0·01.

Data set	R^2	F	Smallest site (ha)
(1) Total species	0·864	$343_{1,54}$	0·000 6
(1) Goldenrods	0·646	$98_{1,54}$	0·002 1
(1) Milkweeds	0·615	$86_{1,54}$	0·002 1
(1) Legumes	0·789	$206_{1,54}$	0·000 6
(2)	0·535	$17_{1,13}$	0·025

maxims (reviewed by Connor & McCoy, 1979). Data sets (1) and (2) show
a significant relationship between species richness and area (Table 1).
Statistics for sets (3)–(5) are provided by Scanlan (1975, 1981), who
reaches similar conclusions. Figure 1 depicts a typical relationship, that
for total species number in set (1). For all five archipelagos, large sites tend
to have more species than do small sites.

One large vs. several small sites

To assess whether one large or several small remnants on average contain
the most species, we used a computer simulation. For each data set, we
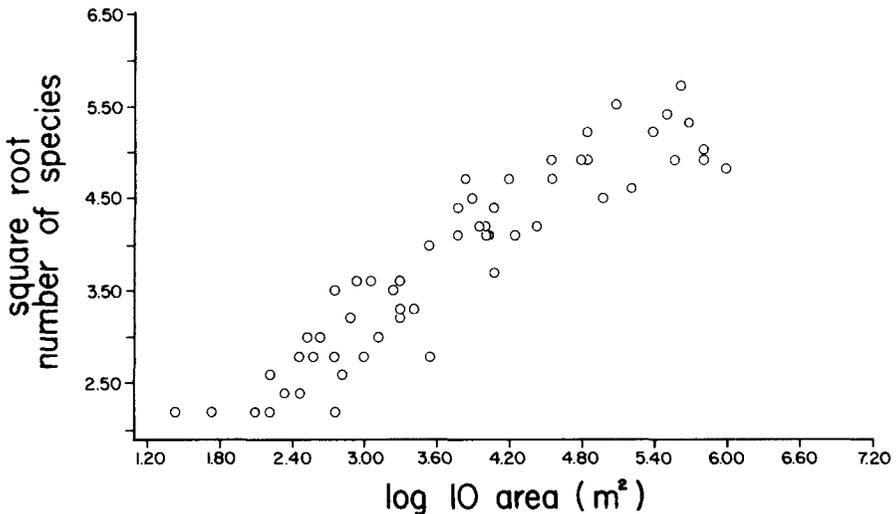

Fig. 1. Species–area relationship for data set (1), *Solidago, Asclepias*, and legume
species in 56 prairie remnants. The regression model is $\sqrt{s} = a + b \log_{10} A$.

TABLE 2

Numbers of Remnants per Simulated Archipelago, Numbers of Archipelagos Constructed, and Significance Levels of Adding Log (Number of Remnants) and an Interaction Term to a Regression of Species Number on Area, for Five Data Sets. The x Variables are Log (Area), Log (Number of Remnants) and an Interaction Term. See Appendix I.

Data set	Maximum number of grouped remnants	Regression transformation	Number of archipelagos constructed	F to enter log number of remnants	Pr	Increase in R^2	F to enter interaction term	Pr
1	10	$\sqrt{S}$	140	34·58	<0·01	0·020	30·12	<0·01
2	5	$\log_{10} S$	19	14·69	<0·01	0·091	0·003	0·96
3	4	$\log_{10} S$	15	24·04	<0·01	0·282	0·669	0·42
4	10	$\log_{10} S$	54	27·90	<0·01	0·106	3·98	0·05
5	5	$\sqrt{S}$	30	14·52	<0·01	0·112	0·749	0·39

randomly lumped together samples of pairs, trios, quartets, etc., of small remnants and compiled species lists of all species in each such random 'archipelago' (Table 2). Appendix 1 details the procedure. None of these random archipelagos was larger in area than the largest remnant. We then performed a multiple regression of number of species on area as first independent variable, number of remnants (including the single remnants) as second independent variable, and the interaction term between area and number of remnants as third independent variable (see Appendix 1). For each of the five data sets, number of remnants still contributed significantly (and positively) to species richness even after effects of area were removed (Table 2). That is, for a given area, on average, the more remnants that constitute an archipelago, the more species. Table 3 provides several specific comparisons (chosen for approximate equality of total area) of single remnants with groups of remnants, for data sets (1) and (3)–(5). Glass (1981, Table 2) gives two

TABLE 3

Several Specific Comparisons of Numbers of Species (S) in Single Large Remnants and Archipelagos of Smaller Remnants, where Area is Approximately Equal. Area in Hectares.

Data set	*Single remnant*		*Multiple remnants*		
	Area	*S*	*Σ Area*	*Number of remnants*	*S*
1	0·066	7	0·059	3	11
1	0·096	8	0·092	3	14
1	0·329	16	0·322	2	16
1	1·750	17	1·749	8	22
1	3·473	24	3·203	2	28
1	96·000	23	93·062	8	31
3	3·810	22	3·650	2	47
3	8·300	32	8·210	2	49
3	10·890	39	10·460	3	49
4	12·270	20	11·970	2	49
4	30·660	33	30·670	4	54
4	75·200	27	73·600	9	76
5	0·790	10	0·780	2	11
5	1·600	10	1·600	3	18
5	3·800	16	3·780	3	21

other comparisons for set (1) demonstrating the general rule that clusters of small remnants have more species than do single large ones.

The interaction term between area and number of remnants is negative for data sets (1)–(4), but significant only for two sets, (1) and (4) (Table 2). It is positive but not significant for set (5). A significant term indicates that the effects of adding a certain number of patches and a certain amount of area to an archipelago are not additive, and the negative sign suggests that there are diminishing returns with increasing numbers of remnants and increasing area (Appendix 1). That is, for data sets (1) and (4), there appear to be an 'optimal' number of patches and 'optimal' areas for an archipelago of remnants, such that species richness increases exceedingly slowly, if at all, above these optima.

Minimum areas

No matter the species richness outcome of one large *vs.* several small remnants, if certain species are absolutely restricted to large remnants, one still might choose single large refuges over archipelagos of smaller ones. Shaffer (1981, and references therein) suggests that a population must respond to four sorts of stochastic events and these set a theoretical lower bound to the viable population size (or area of residence, if one assumes a constant average density). First is demographic stochasticity— chance aspects of survival and reproduction, such as the likelihood that all offspring in some generation will be male. Second is environmental stochasticity, the ordinary range of variation in habitat parameters and sizes of interacting species that a population encounters. Third is the occasional natural catastrophe, like a fire or flood. Fourth is genetic drift combined with inbreeding depression.

Direct evidence for a minimum area on all four grounds is exceedingly scarce, though anecdotes for a few species (e.g., in Shaffer, 1981; Simberloff, 1982a) are compelling. Traditionally the way minimum areas for any species are sought is indirect: one scans a list of occupied sites to see which is the smallest and denotes its area the minimum viable area (references in Simberloff & Abele, 1982). Glass (1981) uses data set (1) in this fashion to conclude that legumes and *Asclepias* can survive in even his smallest remnants ($5 \cdot 7 \, \text{m}^2$), while *Solidago* may require areas at least $50 \, \text{m}^2$. A direct probabilistic test of this premise would be as follows. Given S sites in an archipelago, N_i occurrences by species i, and L_i the size rank of the smallest site occupied by species i, the null probability that an

even smaller site would have been occupied if the N_i occurrences were uniform randomly distributed among sites, independently of site size, is:

$$1 - \frac{\binom{(S - L_i + 1)}{N_i}}{\binom{S}{N_i}}$$

Table 4 lists the numbers of species for each data set for which this probability exceeds 0·05; that is, the number of species that appear to be 'avoiding' small sites. One sees that, for sets (1), (4), and (5), there seems to be a tendency for at least a few species to be excluded from small sites.

However, this entire approach to minimum areas neglects the species–area relationship, and in fact can reasonably be viewed only as setting an upper bound for the minimum area for any species. Assume that no species avoid small sites: species colonisation is analogous to balls randomly falling into buckets with the proviso that the probability that any particular ball falls in any particular bucket is proportional to the size of the bucket. One would still expect rather few species in the smallest sites and some species not found in any small sites. We are saying, in effect, that the observation of a species–area relationship alone, plus the necessity that every species will have some smallest site in which it happens to be found, need not imply that there is some characteristic of still smaller sites that excludes species.

TABLE 4

Number of Species for which the Distribution of Areas of Occupied Sites Differs at Pr $\leq 0·05$ from those of Two Random Colonisation Models. Number of Species Expected to Differ, as a Statistical Artefact, is $0·05 \times$ Total.

Data set	Total number of species	Expected	Number of species for which $Pr(L_i) \leq 0·05$	
			Equal areas model	Unequal areas model
1	39	1·95	23	1
2	152	7·60	5	1
3	102	5·10	1	0
4	116	5·80	10	2
5	84	4·20	8	7

To test whether the distribution of observed minimum areas shows them to be surprisingly large even given the species–area relationship, we used a simulation. For each species i we rained simulated propagules down one at a time onto a set of S simulated buckets, with the size of each bucket proportional to the area of a given remnant. The simulation stopped when N_i of the buckets were occupied (contained at least one propagule). This simulation was run ten times for each data set, and for each species the distribution of observed sizes of occupied remnants was compared by a Kolmogorov–Smirnov test to the simulated expected distribution. Numbers of species that differ from expected at $Pr \leq 0.05$ are given in Table 4. For data sets (1)–(4) there are substantially fewer species than one would have expected for which the distribution of sizes of occupied remnants differs from that produced by a random model. There is thus no evidence that any of the species in these sets avoid small sites, above and beyond the usual species–area relationship. For set (5) there are 7 of 84 species that seem to be arranged non-randomly ($Pr \leq 0.05$) among sites, whereas we would have expected only 4·20 such species. We examined the observed and expected patterns of occurrence for these seven species, and each one is more frequently found in small sites (and less frequently in large ones) than expected. So the conclusion for set (5) is as for the other sets; no data indicate that any species avoid small sites relative to a passive sampling model.

Are small sites depauperate?

A small site tends to have fewer species than a larger site has when all other variables are equal; this is the species–area relationship discussed above. From a conservation standpoint, however, this fact alone is not very useful. Of course if we randomly throw balls at buckets, larger buckets will tend to accumulate more balls. If the balls are of different colours (each colour representing a species), larger buckets will on average have balls of more colours. What concerns us is whether many individual small sites have fewer species than even the species–area relationship would predict, or fewer species than one would have expected if colonisation were random.

The simulation model of the preceding section, in which each species i colonised N_i of the S sites randomly but proportionally to site areas, allows an answer to this question. To estimate the expected number of species $E(X_j)$ for site j, we summed the simulated probabilities, over all species i,

TABLE 5

Numbers of Sites for which Observed Number of Species (X_j) Differs from Expected ($E(X_j)$) by at least Two Standard Deviations.

Data set	Number of sites	$X > E(X) + 2SD$	$X < E(X) + 2SD$
1	56	14	11
2	15	6	3
3	12	5	4
4	22	7	8
5	43	7	8

that site j contains species i. For each species the variance about the probability that it is found at a particular site is the binomial variance, and for each site the variance about $E(X_j)$ is then the sum of variances over all species. When we compare X_j to $E(X_j)$, we find for each of the five data sets substantial divergences (Table 5). The nature of the divergences is identical for all five sets (e.g., Figs. 2 and 3); smaller sites tend to have more species than expected, and large sites tend to have fewer species than expected.
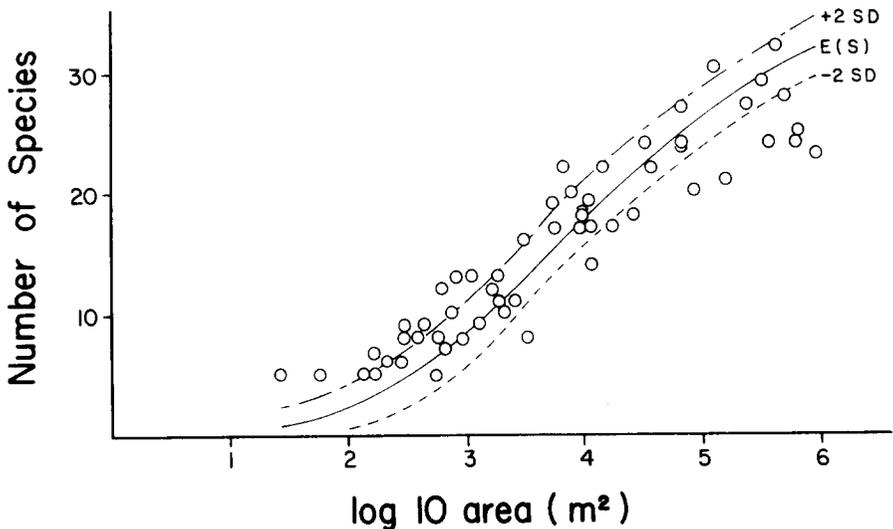

Fig. 2. Observed (circles) and expected (line E(S)) numbers of species for prairie remnants of data set (1).
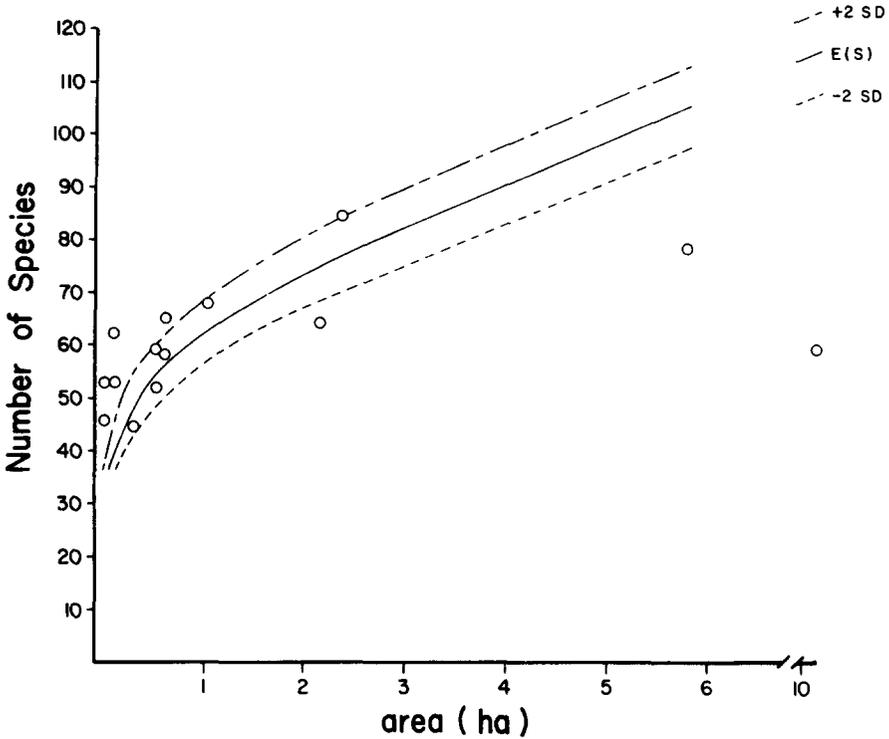
Fig. 3. Observed (circles) and expected (line E(S)) numbers of species for prairie remnants of data set (2).

'Rare' species

Rabinowitz (1981) has recently observed that there are at least seven distinct reasons why a rare plant species may be rare, and a determination of the category to which a species belongs requires intensive autecological research. For our five data sets there is insufficient information to allow this categorisation, but for sets (2)–(5) it is possible for us to define 'rare' operationally as 'found in only one site' and then to examine the distribution of these rare species among sites. For set (1) this assessment is not useful because only three species occupied just one site each.

  We examined the distribution of rare species in two ways. First, we compared by Kolmogorov–Smirnov tests the actual distribution of the rare species to the distributions expected if probabilities of occurrence

TABLE 6

Kolmogorov–Smirnov Statistics and Associated Probabilities for Distribution of 'Rare' Species among Sites of Different Area and among Sites with Different Numbers of Non-rare Species.

Data set	Number of species	Number of rare species	$D_{mn}{}^a$	Pr	$D_{mn}{}^b$	Pr
2	152	45	0·313	<0·01	0·165	>0·10
3	102	36	0·301	<0·01	0·203	>0·10
4	116	31	0·395	<0·01	0·104	>0·10
5	84	36	0·267	<0·01	0·104	>0·10

[a] Kolmogorov–Smirnov test statistic; sites ranked by area.
[b] Kolmogorov–Smirnov test statistic; sites ranked by number of non-rare species.

were proportional to site areas. For all four data sets, these two distributions differed significantly (Table 6), and always in the same direction: smaller sites tend to have more of these 'rare' species than the random model predicts, and larger sites tend to have fewer of them.

Secondly, we asked if the rare species are distributed among sites in a characteristically different way from other species. For each data set we ranked the sites by their numbers of non-rare species, then compared by Kolmogorov–Smirnov tests the distribution of rare species among sites with the distribution of non-rare species among sites (Table 6). For each data set we found no significant difference between distributions. With 'rare' defined as above, rare species colonise small sites disproportionately often, but so do other species.

DISCUSSION

We thus see several recurrent patterns for plants of two prairie archipelagos and herbs of three forest archipelagos. Most important is that groups of small sites tend to have a few more species than do single large sites of equal total area. A number of other taxa display this same pattern (Simberloff, 1982a). Among plants it has been noted by Game & Peterken (in press) for Lincolnshire woodland herbs, Higgs & Usher (1980) for plants of Scottish soft coastal habitats and Yorkshire limestone pavements, chalk quarry reserves, and lowland heaths, Malyshev (1980) for plants of large regions, and Järvinen (1982) for vascular plants of woodlands in the Åland Islands.

We suspect that this pattern derives from the ecological generalisations that each species is restricted to a range of habitats or microhabitats and that species differ in their optimal habitats. In fact, the oldest explanation for the species–area relationship itself has been that larger areas have, on average, more habitats, and that each habitat has an associated set of species (Connor & McCoy, 1979). Other forces may contribute to the species–area relationship (Simberloff, 1976), but surely over all areas but the smallest and most homogeneous, habitat diversity must be the most important variable. One may hypothesise, then, that on average a group of distinct prairie or forest remnants, simply by virtue of spatial separation, will encompass more habitats than will a single refuge of equal total area. Game & Peterken (in press) invoke exactly this explanation for their woodland herb results: a random collection of small woods would likely have more habitats than would one large one. They add that, if one set out deliberately to maximise habitat diversity, one could exaggerate the advantages of a group of small sites by choosing particularly diverse and unusual habitats. Kitchener *et al.* (1980) similarly concluded for lizards of the Australian wheatbelt:

> '...while scattered small reserves, totalling $1 \cdot 78 \times 10^4$ 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.'

Of course, we have no direct evidence for any of our five data sets that habitat diversity is the explanation for our pattern. Such evidence must await autecological and experimental analysis of a large number of the plants.

We recognise that our result—more species in the cluster of small remnants—and its conservation implication run counter to conventional wisdom in the matter (e.g., Whitcomb *et al.*, 1976; Cole, 1981; Frankel & Soulé, 1981), which states that single large reserves are generally to be preferred over clusters of smaller ones. Most authors have followed the lead of Wilson & Willis (1975) in espousing the strategy of single large refuges, arguing that the equilibrium theory of island biogeography

(MacArthur & Wilson, 1967) provides theoretical justification for such a choice. This strategy is suspect because:

(1) The equilibrium theory itself has come under increasing scrutiny and has been demonstrated to depict accurately at best only a few ecological communities (Gilbert, 1980; Simberloff, 1982*b*).

(2) It was quickly shown that the basic equilibrium model, whatever its merits in other settings, offers no prediction whatever about whether one large or several small refuges is optimal (Simberloff & Abele, 1976*a,b*, 1982; Higgs, 1981).

(3) A survey of the few published data relevant to the issue shows that, for a variety of taxa, habitats, and regions, several small sites generally support as many species as one large site, or even more species (Simberloff, 1982*a*; Simberloff & Abele, 1982).

Thus it should be clear by now that conventional wisdom is incorrect in this matter. The empirical evidence contradicts the fundamental equilibrium theory. Available species richness data do not justify the automatic recommendation of single large refuges.

A second pattern is common to all five data sets we studied. There is no evidence that, over the size range of the remnants in these archipelagos, any of the remnants are too small to support any of the species in the species pool. Whatever the minimum viable population sizes for these plants are, they are apparently smaller than can be maintained by even the smallest remnants of these sets (Table 4). Of course many of these remnants are, as remnants, quite young. It is likely that few have been remnants for more than a century. One could, then, reasonably argue that, given a few centuries or millenia, 'relaxation' (Diamond, 1972; Terborgh, 1975) would occur and species richness would fall, as certain species are unable to persist in such small populations. No available data can test this claim, so little more can profitably be said about it. Glass (1981) concludes from a comparison of his prairie remnants (our data set (1)) to species–area curves of quadrats within larger prairies that no relaxation has occurred in this archipelago, while Game & Peterken (in press) conclude on similar grounds that no relaxation has occurred among their herb communities, some of which inhabit woods that became islands a few centuries ago. We are additionally sceptical of long-term relaxation because the phenomenon has never been directly observed and deductions that it has happened in particular instances are beset with

logical and statistical difficulties (Abele & Connor, 1979; Faeth & Conner, 1979).

Finally, a surprising result common to all four data sets that included 'rare' (uniquely occurring) species was that such species tend to be found in small remnants more frequently than a random colonisation model would have predicted, and in large remnants correspondingly less frequently than expected. Järvinen (1982) found a similar result for vascular plant species of the Åland Islands. He noted that, on average, more endangered plant species occur in groups of small islands than on single large ones.

Several possible explanations for this result come to mind; these are not mutually exclusive. One possibility is the 'edge effect'; an ecotone between two habitats frequently contains at least some species from each habitat plus some species not typically found in either (Odum, 1971; Williamson, 1975). On average a group of small refuges would have more boundary or 'edge' than a single large one of equal total area. It could be that the species that we have here defined as 'rare' (namely, uniquely occurring ones) include a large fraction particularly suited to 'edge' habitat. The habitats of most of the species in these four data sets are insufficiently characterised for us to examine this proposition systematically. However, the 'rare' species do not seem to include a disproportionate number that one would call 'edge' species (R. Clinebell, pers. comm.).

A second possibility is that the larger sites have been more intensively managed, to the detriment of many potentially colonising species. This is Helliwell's explanation (1976) of his results for vascular plants of 106 woods of west Shropshire. He found smaller woods on average to have plants more 'valuable' from a conservation standpoint, and attributed this result to the tendency for larger woods to be more intensively managed for timber. We have no data for these four data sets on whether this explanation is feasible.

A third potential explanation is that the small sites might have been maintained as remnants precisely because they contained rare species or unusual habitats. Glass's sites (data set (1)) are on glacial terminal moraines (W. Platt, pers. comm.), which have unusual slopes and drainage patterns. We have no indication for the other data sets that the sites were deliberately chosen to preserve unusual species or habitats.

Fourth, we showed (Table 6) that rare species are not distributed differently from non-rare ones. Small sites tend to have more species of all sorts than one would expect (Table 5 and attendant discussion), both rare and non-rare. So it may well be that the answer to why rare species are

surprisingly often found in small sites is to be found in the answer to a more general question: Why do small sites tend to have surprisingly many species?

CONCLUSION

We conclude, then, that for these forest herb and prairie plant communities, over the size ranges of these remnants, the data clearly imply no justification for preserving single large sites rather than an archipelago of small ones, if such a choice is required. On average a greater species total and more rare species will occur in the archipelago, no species appear to be excluded from the archipelago, and there is no evidence that there will be a short- or long-term decline in species number in the archipelago, particularly if the total area and number of component 'islands' are large. We emphasise three important limitations to our conclusions, all of which constitute calls for a massive amount of autecological research. First, we have not treated habitat diversity in our models. Habitat requirements for most of these plants are not well known, and indeed there is yet no direct demonstration that habitats limit their occurrences in these archipelagos. Second, our conclusions apply only to these communities and sites and should not be transferred to other taxa, size ranges, and regions. Each community must be studied anew. Third, the archipelago strategy must not be carried to a ridiculous extreme. Even though many studies indicate more species in archipelagos (Simberloff & Abele, 1982), at some small size, which must be determined empirically, a multitude of forces must act to render extinction a near certitude (Simberloff & Abele, 1976a, 1982).

Our results should be encouraging to conservation biologists. Even after 80 to 100 years of isolation, these small remnants continue to preserve a diversity of plant species. These findings suggest that management strategies for maintaining small remnants can be successful. Apparently, large continuous areas are not a critical factor for the persistence of many plant species in the prairie-forest ecotone.

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APPENDIX I

We simulated combining groups of remnants and tabulated total species number and area for each group. Up to 5 or 10 remnants were grouped together for each data set (Table 2). Sampling without replacement would

TABLE A-1

Multiple Regression Results for Simulated Archipelagos of Several Remnants. Variables were Forced in a Stepwise Multiple Regression in the Following Order: Area, Number of Remnants, Interaction Term. Transformations were Selected by Examining Residual Plots.

Archipelago	Regression transformation	Intercept	$\log_{10}$(area) coefficient (Δr^2)	$\log_{10}$(number of remnants) coefficient (Δr^2)	Interaction coefficient (Δr^2)
1	$\sqrt{S}$	0·867	0·789, $p < 0·01$ (0·865)	2·378, $p < 0·01$ (0·020)	−0·374, $p < 0·01$ (0·016)
2	$\log_{10} S$	1·72	0·142, $p < 0·01$ (0·714)	0·200, $p < 0·01$ (0·091)	−0·006, $p = 0·96$ (0·000)
3	$\log_{10} S$	1·33	0·184[a], $p < 0·01$ (0·436)	0·750, $p < 0·01$ (0·282)	−0·302, $p = 0·42$ (0·008)
4	$\log_{10} S$	1·26	0·194, $p < 0·01$ (0·615)	0·815, $p < 0·01$ (0·106)	−0·266, $p = 0·05$ (0·014)
5	$\sqrt{S}$	3·30	0·952, $p < 0·01$ (0·346)	1·133, $p < 0·01$ (0·112)	2·041, $p = 0·39$ (0·006)

ensure independence among combinations, but there were too few remnants, so remnants were used in more than one combination.

A potential artefact of lumping many small remnants is that combined areas are often much greater than that of single remnants. Therefore, we generated equal numbers of 2-remnant through 10-remnant combinations, but retained only those that were smaller than the largest single remnant. This restriction has two important consequences: (1) Because the results are unaffected by simulated 'outliers', inferences are valid over the range of the original data. (2) Multiple remnant combinations are often excluded by this procedure, and have relatively little weight in the regressions. From data set (4), for example, we retained eight 2-remnant combinations, but only three 10-remnant combinations.

We did not rely exclusively upon the log–log species–area model, but chose best-fitting transformations by examining residual plots. To assess an exclusive effect of number of remnants, we forced area into the regression model first, to be followed by number of remnants, and then by an interaction term. Transformations, regression coefficients and their significance values, and changes in r^2 are given in Table A-1.

We included an interaction term, $\log_{10}$ area $\times \log_{10}$ number of remnants, in the regression model to assess any non-additive effects of these two variables (Weisberg, 1980). Interaction terms were significant only for data sets 1 and 4 (Table A-1), both of which included 10-remnant combinations. Both of these interaction coefficients are negative, indicating a diminishing return above a certain area or number of remnants. We expect such a result because the species pool will soon become depleted as more and more remnants are added or as area is increased. Our model is:

$$Y = \alpha + \beta_1 X_1 + \beta_2 X_2 - \beta_3 X_1 X_2$$

where $Y = \log_{10} S$, $X_1 = \log_{10}$ area, and $X_2 = \log_{10}$ number of remnants. The fitted least-squares regression coefficients are α, β_1, β_2, and β_3. Differentiating with respect to X_1 yields

$$dY/dX_1 = \beta_1 - \beta_3 X_2$$

Thus, when the slope with respect to $X_1 = 0$,

$$X_2 = \beta_1/\beta_3$$

Above this number of remnants there will be diminishing returns in $\log_{10} S$ for each additional unit of $\log_{10}$ area. Likewise

$$X_1 = \beta_2/\beta_3$$

is the critical area above which there will be diminishing returns for adding remnants. For data set 1, the coefficients yield $X_1 = 228 \cdot 19$ ha and $X_2 = 128$ remnants. For data set 4, $X_1 = 5 \cdot 36$ ha and $X_2 = 1158$ remnants. This critical size for data set 4 is smaller than 68 % of the single remnants. Above a total area of $5 \cdot 36$ ha, there will be a smaller increase in species richness for each remnant that is added. However, these numerical coefficients must not be interpreted literally, because the results depend on the simulation structure.