Biological Conservation **39** (1987) 255–268

A Regional Strategy for Reserve Design and Placement Based on an Analysis of Rare and Endangered Species' Distribution Patterns

Ronald I. Miller*, Susan P. Bratton

Cooperative Parks Study Unit, Institute of Ecology, University of Georgia, Athens, Georgia 30602, USA

&

Peter S. White

Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, Tennessee 37738, USA

(Received 4 September 1985; revised version received 18 August 1986; accepted 26 August 1986)

ABSTRACT

A reserve design strategy was developed for the southern Appalachian region in the United States. The principles for this strategy were derived from analyses of available rare and endangered vascular plant observations and extant topographic heterogeneity patterns. Computer analyses of bounded areas simulating nature reserves demonstrated that area, elevational diversity and slope diversity are important predictors of rare vascular plant species richness. Analysis of the accumulation pattern of new species observations suggested that several unrecorded rare and endangered vascular plant species occur in the region.

A strategy is proposed for the selection and placement of nature reserves, conformable to particular biogeographic regions. Our scientific understanding of the dynamic processes governing insularity is too incomplete for incorporation into current regional conservation planning. A model of land purchase costs was compared in terms of expense per species acquired for reserves of different sizes and shapes. Economic considerations need to be integrated with biological conservation concerns to achieve the most tractable strategy.

* Present address: Geographisches Institut, University of Zürich-Irchel, Winterthurerstrasse 190, 8057 Zürich, Switzerland.

INTRODUCTION

There has been considerable debate recently concerning the correct reserve design strategy for the long-term preservation of plant species. The discussion has centred on the benefits of various size and shape design criteria for nature reserves (Simberloff & Abele, 1984; Willis, 1984). Recent evidence suggests that the natural history characteristics and population biology of individual plant species (Järvinen, 1982) and patterns of habitat dispersion within and among sites (Simberloff & Gotelli, 1984) may be more influential predictors of regional plant species richness patterns than generalised size and shape criteria.

Species–area relationships represent dynamic features of changing species distributions. The characteristics of species–area relationships are regulated in individual taxa and biogeographic regions by diverse spatial and temporal processes (Higgs & Usher, 1980). Evidence suggests that reserve size may not be a predominant factor influencing plant species richness and composition (Simberloff & Gotelli, 1984). Since principles which maximise plant diversity within reserves will be one objective of conservation considerations, regional guidelines for reserve design should be predicated upon the critical biological and habitat factors influencing extant patterns of species richness.

Within the next 50 years, landscape patterns in many regions of the United States will be established to the degree that any natural areas not previously set aside for conservation purposes will be developed. It is unlikely that the necessary botanical surveys will be conducted in time for conservationists confidently to design natural reserves which optimally protect endangered plant species. Therefore, decisions about regional botanical conservation requirements and necessary alterations in prevailing patterns of regional nature reserve design and placement demand the use of current botanical knowledge about vulnerable plant resources and habitats.

Within a biogeographic province, the majority of the regional variance in plant diversity is attributable to rare plant species. In other words, changes in plant species richness are primarily dependent on rare and endangered species' distribution patterns, rather than on the distribution patterns of the most common and abundant species. Since the maintenance of diversity patterns for the plant species within a region is a prominent conservation goal, the use of rare and endangered plant species observations for the development of regional conservation guidelines is particularly important.

An analysis of rare and endangered vascular plant distributions in the southern Appalachians was performed to examine postulated design criteria. The goal was the identification of criteria which would maximise vascular plant species diversity in nature reserves within this temperate region of high floral diversity. Since the cost of land acquisition is an important factor in reserve design, a simple cost model was also used to evaluate design criteria in terms of cost per rare species included within a reserve. Reserve guidelines were developed both for the southern Appalachians and as a generalised model for biogeographic regions.

STUDY AREA AND METHODS

The primary study area was the central portion of the southern Appalachian region located between 34° 30′ and 36° 50′ N Latitude and 81°07′ and 86°45′W Longitude in the southeastern United States. This area was further divided into six subregions for purposes of analysis (Miller, 1986). An extensive compilation of rare and endangered vascular plant observations from this region was obtained from the Heritage Group at the Tennessee Valley Authority (Norris, Tennessee, USA). This represented the most complete documentation of plant species observations for this region (Miller, 1986). Plant species in this data set were included based on their incorporation in state and federal rare and endangered vascular plant listings. The southern Appalachians contain more than 2200 native vascular species. Great Smoky Mountains National Park alone contains 1500 native vascular species.

Rare plant diversity patterns within the southern Appalachians were analysed from these data and criteria for assessing regional conservation strategies were derived. This digitised set of species observations was analysed in conjunction with regional habitat heterogeneity distributions derived from digitised topographic, geologic and geographic data. A series of regular polygons representing simulated park areas in the region (Fig. 3 —Miller, 1986) were geographically projected by computer upon both the species and habitat distribution data. Rare plant species and habitat diversity values generated from these data became identified with each simulated park area. Statistical analyses determined the relationship between species richness and measures of topographic, habitat and geographic diversity within each simulated park area. To test the hypothesis that a number of smaller reserves may contain a greater number of species than a single, large reserve of equal size, simulated park areas were designed to permit comparisons of area combinations. This provided a measure of current conditions within bounded areas of the southern Appalachians; no inferences were made about the long-term effect of insularisation, which was the focus of the previous studies (Simberloff & Abele, 1976, 1982).

Similarity indices were calculated for each of the simulated reserve areas. Species similarity index values were compared to ascertain species compositional similarity between simulated park areas. Czekanowski's Quantitative Index was chosen as the most statistically unbiased estimate for compositional similarity available (Bloom, 1981). This index has been extensively used for comparison of samples in ecological studies (Whittaker, 1973), and the following formula was used in this study:

$$CZ_{ik} = 2\frac{\sum_{j=1}^{s} \min(x_{ij}, x_{kj})}{\sum_{j=1}^{s} (x_{ij} + x_{kj})}$$

where x_{ij} = occurrence of the jth species in the ith park area, x_{kj} = occurrence of the jth species in the kth park area and s = total number of rare and endangered species occurring in all park areas (i.e. over the entire region).

Land value was related to many variables including accessibility, presence of streams, tillability, fertility and the presence of harvestable natural resources. Currently in the southern Appalachians, tourist development has increased the cost of land that could not profitably be farmed. The important variables that determine the cost of land in this regard include views, proximity of paved roads and presence of streams. In general, however, land values tended to decrease with increasing elevation and slope. Although land prices vary greatly throughout the region, an investigation of local newspapers in east Tennessee indicated that rich valley bottoms at low elevations cost roughly \$10 000 to \$12 400 ha^{-1}, low ridges and slopes above the valleys cost \$5000 to \$7400 ha^{-1}, and inaccessible and steep sites cost \$2500 or less ha^{-1} in larger tracts. Three models were tested that reflect cost decline with increasing elevation and slope. The models all provided similar results, thus only one is presented here. The following linear model estimates the comparative cost (artificial cost units) of acquiring each of the simulated park areas for each of the subregions:

$$\text{Cost per grid cell} = 5{\cdot}5 - (0{\cdot}125 \times \text{elevation class})$$

where 300 m was used as the minimum elevation class and each subsequent class represented an increase of 50 m. Each grid cell represented $2{\cdot}07 \times 10^5\ m^2$. Cost per each grid cell was calculated and then summed for each simulated park. Using this model, predicted park cost was compared to the number of rare species within each simulated park.

RESULTS

Species diversity patterns

In the majority of instances, a group of smaller areas contained an equal or greater number of rare and endangered vascular plant species than did a single large reserve area (Table 1). The comparison between the 'A4' and the 'C' park areas was most indicative, since these were comparisons between a single large area and a group of smaller non-contiguous areas (Table 1). Based on these species–area comparisons, an archipelago of smaller reserves will maximise rare and endangered plant species richness in the southern Appalachians under current conditions.

Some patterns are evident from the diversity values identified with the largest simulated reserves in each of the six subregions of the southern Appalachians (Table 2). A significant relationship clearly existed between magnitudes of species richness and elevation and slope diversity. When statistical analyses were performed on the data from all simulated reserves, this became apparent (Table 3). Only subregion 10 appears to be somewhat of an outlier in regard to this relation.

Results from univariate regression analyses (Table 3) indicated the appropriateness of a reserve design strategy for the southern Appalachians

TABLE 1

Comparative Species Richness Results from Some Equivalent Simulated Park Area Combinations in the Southern Appalachian Region

(All numerical results represent the number of rare and endangered plant species recorded within single and multiple parks of equivalent area. The simulated park areas were of the following sizes: $A1 = 4396\,km^2$, $A2 = 3296\,km^2$, $A3 = 2198\,km^2$, $A4 = 1110\,km^2$, $B1 = 2202\,km^2$, $C1 = C2 = C3 = C4 = C5 = C6 = 184\,km^2$.)

Park designation:	*A1*	*2 × A3*	*B1*	*2 × A4*	*A4*	*C1 + C2 + C3 + C4 + C5 + C6*
Area within simulated parks (km^2):	*4396*	*4396*	*2202*	*2220*	*1110*	*1104*
Southern Appalachians subregion						
1—Smokies	60	102	51	84	42	47
2—Clinch Mt	9	14	4	10	5	5[a]
3—Blue Ridge–Cherokee Nat. Forest	17	28	12	24	12	11[a]
4—Pisgah–Stone Mts	47	46	18	24	12	14[a]
5—Cherokee Nat. Forest	46	38	14	20	10	15[a]
10—Blue Ridge–Pisgah	41	26	26	22	11	14[a]

[a] There were always <six parks with recorded species observations represented in each of these areas.

TABLE 2

Variable Values Associated with Each of the Largest Park Simulation Areas in the Six Subregions Comprising the Southern Appalachians

(Subregions are listed by the magnitude of the species richness values. All topographic diversity values were calculated from the Shannon–Wiener index. Similarity values were calculated from Czekanowski's index and represented the average similarity value based on comparisons with the largest park simulation areas in the other southern Appalachian subregions. Adapted from Table 5 in Miller (1986).)

Subregion number	*Species richness*	*Total number of observations*	*Elevational diversity*	*Slope diversity*	*Aspect diversity*	*Species similarity*
1—Smokies	60	278	4·74	2·65	2·97	0·17
4—Pisgah–Stone Mt	47	93	4·16	2·14	2·97	0·20
5—Cherokee Nat. Forest	46	148	3·73	1·71	2·93	0·29
10—Blue Ridge–Pisgah	41	130	4·26	2·49	2·98	0·29
3—Blue Ridge–Cherokee Nat. Forest	17	40	3·53	1·60	2·96	0·06
2—Clinch Mt	9	15	2·15	1·13	2·92	0·07

which incorporates the multiplicity of factors influencing plant species distributions. When area was removed as a factor, univariate models utilising elevational diversity or slope diversity as independent variables explained a significant proportion of the remaining variability in rare species richness within the simulated reserves.

There was a clear distinction between the results associated with the six smaller areas of equal size ($184\,km^2$) and results associated with the six larger park areas of varying sizes (see Table 1 for these area values). The smaller areas exhibited higher variability in values of species richness, topographic diversity and species similarity. Given the regional scale and the 1008 verified observations from the study area, this variability was not surprising. The statistical variability in the sampling of the smaller park

TABLE 3

The Most Statistically Significant (highest r^2 adjusted values) Univariate Models of Rare and Endangered Vascular Plant Species Richness in the Southern Appalachians (from Miller, 1986).

Dependent variable	*Independent variable*	*F value*	*r^2 adjusted*	*$p > F$*
Log (species richness)	Log area	25·46	0·46	0·000 1
Log (species richness)/Log (area)	Exp (elevation diversity)	93·08	0·74	0·000 1
Log (species richness)/Log (area)	Slope diversity	40·57	0·55	0·000 1

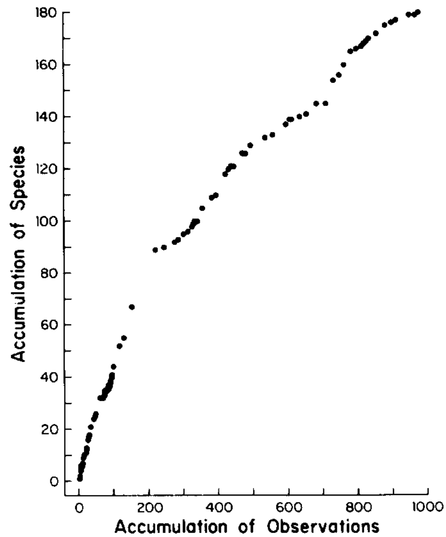

Fig. 1. Accumulation of previously unrecorded vascular plant species in relation to the accumulation of rare plant species in the southern Appalachians study region.

areas indicates the lessening of importance of area size as a predictor of rare plant richness at this scale.

The accumulation of new species (previously unrecorded) observations in relation to the accumulation of all rare and endangered vascular plant observations for the region was plotted (Fig. 1). Of the original 1008 observations, 976 records representing 180 species included interpretable observation dates. The two plateaus represented reduced levels of collecting intensity due to historical factors. The rate of documentation of rare and endangered vascular plant species initially increased exponentially and has significantly slowed since the onset of botanical collecting in the southern Appalachians. A greater intensity of botanical collecting in the future will document significantly fewer rare and endangered plant species in the region.

Environmental heterogeneity

For the southern Appalachians region, the following were the average similarity properties for all the pairs of simulated park areas of equal size (similarity indices were only calculated for areas of equal size):

Average similarity between all pairs of areas = 0·14
Similarity of the most similar pair of areas = 0·67
Similarity of the least similar pair of areas = 0

TABLE 4

Results of a Linear Regression which Compared Land Costs per Rare Species with Elevation

(In each subregion, the first column represents relative cost per species. Cost per species is the estimated cost of the reserve, divided by the number of rare species found there (Table 1). The second column represents the relative cost per species as a percentage of the cost in the 'A1' reserve, e.g. cost per species of 'A4' divided by cost per species of 'A1'.)

Park designation	*Subregion identification number*											
	1		*2*		*3*		*4*		*5*		*6*	
	Cost/sp.	*%*	*Cost/sp.*	*%*	*Cost/sp.*	*%*	*Cost/sp.*	*%*	*Cost/sp.*	*%*	*Cost/sp.*	*%*
A1	1 187	100	10 481	100	5 318	100	1 482	100	1 834	100	1 749	100
A4	308	26	5 878	56	1 850	35	1 341	90	2 224	121	1 588	91
B1	648	55	11 881	113	3 708	69	1 878	126	3 996	218	1 293	74
C combined[a]	380	32	1 669	16	716	13	829	56	1 262	69	857	49

[a] Reserve areas with zero species observations were deleted in this analysis.

A similarity value was computed for each of the largest simulated park areas within each of the southern Appalachian subregions (Table 2). The least diverse simulated reserves (i.e. lowest elevation and slope diversities) exhibited the lowest similarity with other reserves. This reinforces the importance of topographic heterogeneity in relation to the distribution of rare and endangered vascular plants in the southern Appalachians.

Cost of reserves

Table 4 shows the cost of acquisition per rare species for the cost model predicted on declining cost with increasing elevation. In all the cost models, cost per species was least in the Great Smoky Mountains, both because of its high density of rare species and high elevations. In this subregion, the 'A4' reserve simulation, representing a single, small park in the centre of the range, was the least expensive reserve per species protected. The cost per species of the 'A1' reserve simulation, with much greater area, was four times that of the core 'A4' reserve. Subregions 2 and 3, which had 15% and 28%, respectively, of the species richness of subregion 1, exhibited relatively expensive cost models due to low densities of species and low elevations. In subregions 4 and 5, however, the 'A4' reserve was not as cost-effective as 'A1' reserve.

In all cases except subregion 4, the cost per species in the 'C' reserve areas was less than the cost per species in the 'A1' reserve. The model representing an equal cost per unit area produced a decrease in the cost distinction between subregion 1 and subregions 2 and 3. However, a series of small reserves, represented by the group of 'C' reserve areas, was again the least expensive reserve strategy in terms of per species cost.

DISCUSSION

The use of cause and effect relationships between species richness and dynamic processes (e.g. nutrient cycling, succession, immigration and extinction) to explain changes in species richness due to insularity requires significant further scientific documentation and research. Currently these processes can be best understood within individual reserve areas. Therefore, when possible, the influence of these dynamic processes on populations and communities within single reserves should be considered in more long-term park management plans.

The rate of development and procurement of land within the southern Appalachians will likely make the selection and design of nature reserves obsolete within the next 30–50 years. Analyses of regional landscape patterns and extant rare species distribution patterns (Miller, 1985; Feoli & Orlóci, 1985) can be used for the development of regional reserve selection and design criteria. Such an analysis approach was used to develop a regional strategy for the design and selection of nature reserves in the southern Appalachian region.

Five of the most commonly cited scientific criteria (Margules & Usher, 1981) for assessing the conservation value of natural areas are diversity, area, rarity, naturalness and representativeness. In this southern Appalachians study, three of these five criteria were analysed in relation to the regional conservation strategy proposed here (Table 5). Within a region, composite indices of conservation value for natural areas can be developed based on the regional importance values assigned to each of these primary criteria.

The species–area relationship explained the greatest percentage of the variability in species richness in the Smokies subregion (Miller & White, 1986). The value of the species–area relationship is substantially dependent on the degree to which increases in area reflect increases in environmental heterogeneity within a region (Boecklen & Gotelli, 1984; Miller, 1986). In the southern Appalachians, the maximum degree of topographic

TABLE 5
Proposed Regional Analysis Approaches for Quantifying the Importance of Criteria for the Conservation Assessment of Natural Areas

Scientific criteria	*Regional analysis approaches*
Area	Analysis and determination of species area patterns for the taxa under consideration.
Diversity	Analysis of species diversity patterns across the region (with emphasis on rare and endangered species for the critical taxa). Analysis of the dominant and critical environmental diversity patterns (e.g. climatic, topographic, geologic, etc.).
Rarity	Determined from regional species distribution patterns or from previously existing governmental and private listings of rare species. A definition of the scale of rarity will need to be made.
Naturalness[a]	Historical and current land use records used to determine the various levels of human impact experienced by the regional landscape components.
Representativeness[a]	The composition of a regional landscape analysed in terms of different successional stages, vegetation types, degrees of human impact, etc. Determination of how a regional reserve ensemble can best represent the patterns characteristic of a region.

[a] These criteria, included as part of the regional conservation strategy, were not, however, considered during the southern Appalachians analysis.

heterogeneity occurred in the Smokies subregion (Table 3, Miller, 1986) and this was also the region where the strength of the species–area relationship was maximised. In the Smokies subregion, therefore, when biology alone is considered, maximisation of areal extent is the best conservation strategy for maximising both species richness and habitat heterogeneity.

The use of strictly biological criteria for reserve selection suggests that simulated reserve design 'A1' is the optimal one for the Great Smokies subregion. In the consideration of cost question, however, the 'A4' design might be superior because, given equal available funds, this would purchase more species. The consideration of cost questions the value of establishing large reserves for rare plant species, at least when preservation of other types of species, such as large predators, is not a primary conservation goal. Especially in the case of ridge-top endemics, where large buffer zones are probably of limited value, better genetic conservation might be obtained by buying several small reserves, all containing rare species habitat. If finances are limited, a series of small reserves in areas of high environmental heterogeneity will preserve more species per unit expenditure than will a single, large reserve in the centre of the area. The large reserve is, however, biologically more desirable.

Based on this study, the following reserve design strategy in the southern Appalachians is suggested. The largest reserve(s) within a region should be located in the area which exhibits the strongest species–area relation (i.e. highest r^2 adjusted value) in regard to the rare and endangered species in that biogeographic region. Outside this area, reserves should be located, regardless of size, in areas which maximise the contained environmental heterogeneity which has statistically been shown to give the most effective prediction of rare and endangered species richness.

The design strategy of maximising reserve area in the Smokies region and maximising reserve environmental heterogeneity in other parts of the southern Appalachians is relevant to this biogeographic region. The methodological approach developed in this study may be applied to other biogeographic regions and taxa. For example, in a different region, edaphic features may best predict rare species distribution or the species–area model may predominate throughout the region. In these circumstances, a very different reserve design strategy will result.

A recent study utilised a similar sampling methodology on a smaller spatial scale to analyse plant species diversity patterns in British woodlands (Peterken & Game, 1984). This analysis also involved a predefined subcategory of woodland plants. Both studies conclude that factors other than isolation and area must influence the plant species richness patterns. Both analyses conclude that area may act as a composite predictor of habitat heterogeneity.

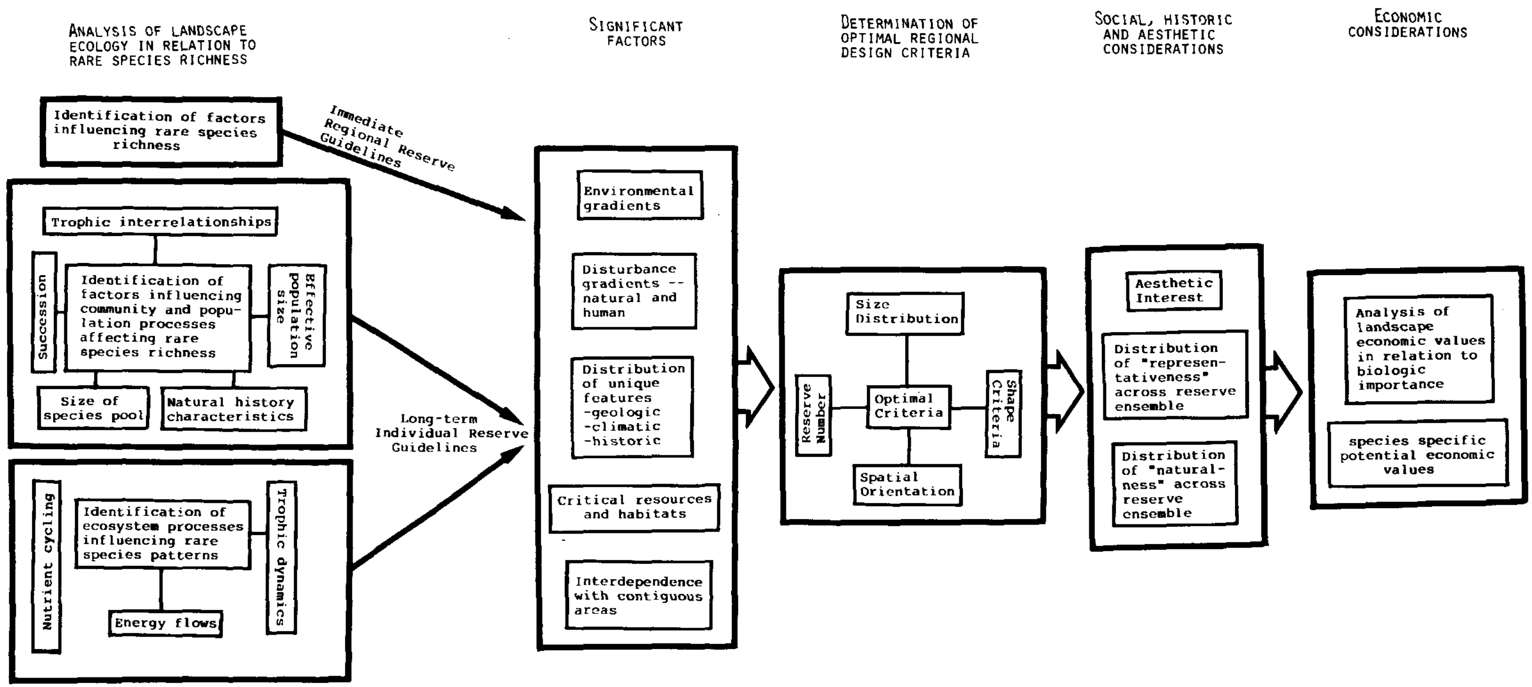

Fig. 2. A systematic procedure for the selection of a reserve ensemble within a biogeographic region, based on optimising the inclusion of rare and endangered species. Dynamic processes influencing population, community and ecosystem structure and function will only be considered in long-term planning for individual reserves.

This study produced a systematic approach for the selection and design of natural areas from an analysis of environmental, species and economic data (Fig. 2). Even with a less than complete data base, conclusions can be made about reserve number, size and placement. Conservation strategy will also depend upon knowledge of areas of unique conservation value obtained from field naturalists and historical records. Ultimately, a final regional conservation plan will combine the results of a model inferred from botanical data with the results of a regional evaluation of wildlife habitat requirements (Asherin *et al.*, 1979).

The methodology developed in this study provides a tractable means of modelling extant species distribution patterns. This provides a useful approach to current park planning. However, insularity will likely influence rare species distributions in the future and should be considered in relation to the conditions influencing specific reserves. Also, for taxa with very different characteristics (e.g. mobile, large predators), individual species range distributions will play a more crucial role in determining specific reserve design strategies.

REFERENCES

Asherin, D. A., Short, H. L. & Roelle, J. E. (1979). Regional evaluation of wildlife habitat quality using rapid assessment methodologies. *Trans. N. Am. Wildl. nat. Resour. Conf.*, **44**, 404–24.

Bloom, S. A. (1981). Similarity indices in community studies: Potential pitfalls. *Mar. Ecol. Prog. Ser.*, **5**, 125–8.

Boecklen, W. J. & Gotelli, N. J. (1984). Island biogeographic theory and conservation practice: Species–area or specious-area relationships? *Biol. Conserv.*, **29**, 63–80.

Feoli, E. & Orlóci, L. (1985). Species dispersion profiles of anthropogenic grasslands in the Italian eastern Pre-Alps. *Vegetatio*, **60**, 113–18.

Higgs, A. J. & Usher, M. B. (1980). Should nature reserves be large or small? *Nature, Lond.*, **285**, 568–9.

Järvinen, O. (1982). Conservation of endangered plant populations: Single large or several small reserves? *Oikos*, **38**, 301–7.

Margules, C. & Usher, M. B. (1981). Criteria used in assessing wildlife conservation potential: A review. *Biol. Conserv.*, **21**, 79–109.

Miller, R. I. (1985). *Distribution patterns of rare and endangered flora in the southern Appalachians.* PhD dissertation, University of Georgia, Athens.

Miller, R. I. (1986). Predicting rare plant distribution patterns in the southern Appalachians of the south-eastern USA. *J. Biogeog.*, **13**, 293–311.

Miller, R. I. & White, P. S. (1986). Considerations for preserve design based on the distribution of rare plants in Great Smoky Mountains National Park, USA. *J. environ. Mgmt*, **10**, 119–24.

Peterken, G. F. & Game, M. (1984). Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.*, **72**, 155–82.

Simberloff, D. S. & Abele, L. G. (1976). Island biogeographic theory and conservation practice. *Science, N.Y.*, **191**, 285–6.
Simberloff, D. & Abele, L. G. (1982). Refuge design and island biogeographic theory: Effects of fragmentation. *Am. Nat.*, **120**, 41–50.
Simberloff, D. & Abele, L. G. (1984). Conservation and obfuscation: subdivision of reserves. *Oikos*, **42**, 399–401.
Simberloff, D. & Gotelli, N. (1984). Effects of insularization on plant species richness in the prairie-forest ecotone. *Biol. Conserv.*, **29**, 27–46.
Whittaker, R. H. (1973). *Ordination and classification of communities*. The Hague, Junk.
Willis, E. O. (1984). Conservation, subdivision of reserves and the anti-dismemberment hypothesis. *Oikos*, **42**, 396–8.