Quantifying Plant Diversity in Zion National Park, Utah

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Abstract—The vegetation of Zion National Park (ZNP) is used to illustrate the use of various indices that describe aspects of botanical diversity. The simplest method reports the average number of vascular species per 0.01 ha (0.025 acre) macroplot. The MacArthur-Wilson index of diversity is given for each plant community of occurrence in the Park. Neither the number of species per macroplot nor the MacArthur-Wilson index show much variation among the plant communities of the Park. A third index shows the proportion of a community's major species that reach maximum regional abundance in that community. This index records large differences among communities and is indicative of the amount of genetic diversity inherent in a community. Such information will be of interest to evolutionists, plant breeders, and horticulturists. A fourth index quantifies the degree to which major species of a community are rare elsewhere in the region. This rarity index also shows large differences among the communities considered. Since rarity has unusual appeal to humans, this index identifies communities of particular interest to users and managers. Vegetational composition upon which all indices are based is reported for the 10 major communities of ZNP. Procedures for computing each index are given.

Most conservation efforts of the past have focused on individual species. Such activities have emphasized the life cycle, reproductive biology, and habitat requirements of individual species. Those studies have often resulted in greatly enlarged populations and improved habitat for species in danger of extinction. Nevertheless, conservationists have increasingly called for preservation of entire biotic communities and habitats associated with them (Owen and others 1998).

A large literature has developed around the general theme of preservation of individual species. Included are rigorous methods for quantifying genetic diversity of individuals and populations, for estimating population size, and for evaluating the likelihood of extinction in future time periods of variable length (Primack 1998). In contrast, little attention has been directed to procedures for quantifying the degree to which various natural communities are threatened, the likelihood that they harbor rare species or contain unique genotypes, or are the habitat of species vulnerable to extinction. Greater effort has been devoted to development of procedures for describing characteristics of individual plant communities (Whittaker 1975).

This paper represents an attempt to quantify various aspects of the biodiversity of the plant communities of Zion National Park (ZNP). Our analyses are based on a large vegetational sample drawn from throughout ZNP, an area that covers approximately 60,000 ha in southwestern Utah. Since the Park extends over an area of variable geology and diverse topography, plant communities adapted to very different microenvironments are represented in the sample.

Methods

Our sample is based on 0.01 ha macroplots placed at the intersection of a 1.61 km (1.0 mile) grid across the entire surface of ZNP. In all, 309 macroplots were thus sampled within the Park. Since essentially the entire area of concern has been covered by the United States land survey, we used U.S. Geological Survey, 7.5 min quadrangle, topographic maps to locate the site of each section corner in the field. Workers visited each corner and delimited a circular macroplot centered on the corner.

At each section corner (or as near that point as topography would permit), a macroplot was inventoried using procedures similar to those developed by workers at the Zurick-Montpellier School of Phytosociology (Braun-Blanquet 1932). At each plot, all vascular species rooted therein were recorded and foliage cover (projected crown) of each was visually estimated. Workers also recorded elevation, aspect, and slope at each plot. Geologic substrate at the site, seral state of the vegetation, and evidence of prior disturbing influences (such as domestic grazers, logging, abandoned roads or trails, wildfire, and so forth) on the plot were recorded. Finally, the worker made an estimate of composition of the living cover (percentage of the total contributed by lifeform groups such as trees, shrubs, perennial broadleaved-herbs or graminoids, annuals, or nonvascular species) and the abiotic surface (relative cover of bare soil, consolidated rock, rock pavement, boulders, or litter).

Since some of the plant communities of occurrence within ZNP are of very limited area there (for example, abandoned fields, riparian forests, and hanging gardens), we have arbitrarily selected sampling points in those community types that do not fall on section corners. All well-developed hanging gardens encountered that approached 0.01 ha in area were sampled. Within the abandoned fields and riparian

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community types, a stratified-random method was used to select additional macroplot locations when section corners within the type were few in number. Plant nomenclature follows Welsh and others (1993).

Since our study utilized concepts and indices not commonly employed among land managers, we have provided a list of terms and indices used as we prepared this manuscript. Words and terms are defined and procedures given for computing the four indices that we use (table 1).

Results

We have recognized 10 plant communities in ZNP (table 2). Criteria for recognition were those commonly used by land managers in the area. Most of the community types could be justifiably further subdivided, but such fragmentation quickly results in sample sizes that are too small to permit reliable statistical tests of differences

Table 1—Definitions of words or terms used to describe the various indices computed to characterize aspects of plant diversity of the several plant communities recognized in Zion National Park. Procedures for computing the four indices are also given.

Word or term	Definition or computational procedures
Modal species	Prevalent species that reach maximum regional commonness in the community in question (Curtis 1959).
Percentage presence	The percentage of all macroplots placed in each community type that included rooted individuals of species X.
Prevalent species	The commonest species in a particular community type selected in a number equal to the species density for that community. All species encountered in the full sample for a community are arranged in decreasing order of percentage presence. Prevalents are selected from the top of that list in a number equal to average species density for the community. The number is rounded up to the nearest whole number (Curtis 1959).
Species density	The average number of species occurring in the macroplots of any particular community type (Curtis 1959).
Index Computation	
Diversity	Diversity (D) = $1/\sum pi^2$ where p = the decimal proportion of the sum of percent of presence of all prevalent species in the community contributed by each prevalent species. D is an approximation of the number of species of equal commonness in the community (MacArthur and Wilson 1962).
Distinctiveness	Distinctiveness = $\frac{\text{no. modal prevalent species}}{\text{no. prevalent species}} \times 100$ (Curtis 1959)
Rarity	The number of occurrences of each community prevalent in the entire study (309 macroplots) is expressed as a decimal fraction of the total of plots observe (309). The reciprocal of each fraction is taken. These reciprocal values are summed across all prevalent species of any given community and their average value is obtained. That average is taken as the rarity index for that community.

Table 2—The 10 plant communities recognized in Zion National Park, the gross characteristics of their environments, the relative area of each within the Park, and sample size by community are presented here. Aspects of the soils associated with each community can be found in Mortensen and others (1977).

Community	Percent of Park area	Average elevation (m)	Predicted annual precipitation[a] (cm)	Percent of coverage of bare rock	No. macro-plots
Blackbrush (CORA)	1.7	1,261	~25.4	10.9	10
Abandoned fields	0.6	1,366	~25.4	0.1	6
Riparian	1.5	1,490	~25.4	12.6	19
Hanging gardens	Trace	1,505	~25.4	27.2	23
Sagebrush (ARTR)	2.4	1,510	~32.6	4.9	7
Juniper- pinyon (JUOS-PIMO)	46.5	1,700	~38.1	20.1	108
Rock crevice	19.1	1,770	~38.1	60.6	25
Mountain brush	13.9	1,946	~45.6	8.5	57
Ponderosa pine (PIPO)	8.3	1,970	~45.6	14.2	33
Douglas-fir-white fir (PSME-ABCO)	6.1	1,997	~50.8	9.3	21

[a]Based on a regression equation developed by Harper (1993) using data from stations of known elevation and precipitation in the general region of ZNP.

observed between subunits. We have elsewhere (Harper 1993) suggested habitat-type subdivisions for the major communities that are likely to be useful for management.

The communities recognized in the Park range in elevation from an average of 1,261 m (blackbrush or *Coleogyne ramosissima* community) to almost 2,000 m (Douglas-fir/white fir or *Pseudotsuga menziesii*/*Abies concolor* forests). Precipitation averages from about 25 cm per year in the blackbrush shrub deserts to over 50 cm per year in the mixed conifer forests (table 2). Since the Park covers an area of rugged, rapidly eroding terrain, most of the plant communities occur on very rocky sites. The rock crevice community, as recognized here, averaged over 60 percent of bare rock on constituent sites, and only four communities showed less than 10 percent bare rock (table 2).

The commonest communities in the Park were juniper-pinyon (46.5 percent of the surface area of the Park), rock crevice (19.1 percent of the Park), and mountain brush (13.9 percent). Five communities individually covered less than 3.0 percent of the area of the Park: uncommon communities arranged in order of increasing area included hanging gardens, abandoned fields, riparian, blackbrush, and sagebrush (table 2).

We summarize data for occurrence (percent presence in the macroplots of each community type) of all prevalent species in the 10 communities recognized in the Park in table 3. Although 929 plant taxa have been collected in ZNP [based on a checklist prepared by Kaye Thorne (1989) and collections made during the course of the field work for this report], only 514 taxa occurred in the macroplots inventoried

Table 3—Prevalent species performance in 10 plant communities of Zion National Park. The values reported are percentage occurrence in the 0.01 ha (0.025 acre) macroplots placed in each community. Values are underlined in communities where the species is prevalent and underlined and bold where the species are both prevalent and modal. See table 1 for definitions of the terms prevalent and modal. All results reported here are derived from a report by Harper (1993).

Species	CORA	Aband. fields	Riparian	Hang. garden	ARTR	JUOS PIMO	Rock. crev.	Mt. brush	PIPO	PSME ABCO
Woody										
Abies concolor			16	20			4	5		**52**
Acer grandidentatum			37	40		1		14	6	**43**
A. negundo			**63**	60			4	2		10
Amelanchier utahensis				40	14	**65**	56	49	64	62
Arctostaphylos patula			5	20		38	60	35	**61**	10
Arenaria macradenia			11			16		18	**24**	19
Artemisia tridentata	10		5		**100**	26		19	18	
Atriplex canescens		**33**			14	1				
Cercocarpus intricatus			5	20		5	**84**	7	21	24
Chrysothamnus nauseosus	20	17	16		**43**	13	16	16	12	5
Coleogyne ramosissima	**100**					5		2		
Ephedra nevadensis	**40**					9	4			
Fraxinus anomala			5	20		27	12	12		**29**
F. velutina			**32**							
Gutierrezia microcephala	**80**	50	21	20						
G. sarothrae					**71**	44	36	21	21	
Haplopappus scopulorum					14	19	4	12	15	**38**
Holodiscus dumosus			16	20			32	2	3	**33**
Juniperus osteosperma	60	33		20	14	**82**	12	19	18	
J. scopulorum			5	20		1		19	9	**24**
Lycium pallidum		**33**								
Mahonia repens			16	20		6		12	12	**38**
Opuntia macrorhiza	30		11		29	53	**56**	44	49	24
O. phaeacantha		17			**29**	2		5	3	
Pachystima myrsinites			11	60		12	4	23	24	**71**
Petrophytum caespitosum			5	**39**			28		3	10
Pinus edulis				20		**34**	4	12	15	19
P. monophylla	40		5			**53**		12		
P. ponderosa			5	20		2	56	11	**97**	29
Phlox austromontana			5		14	15	20	30	**39**	5
Populus fremontii			**32**							
Pseudotsuga menziesii			11	40			4	2	3	**48**
Psorothamnus fremontii	**30**				14	5				
Purshia tridentata			5	20		14	4	19	**30**	5
Quercus gambelii		17	37	60		34	24	75	67	**86**
Q. trubinella			5			30	**32**	16	12	
Symphoricarpos oreophilus			11			13	4	46	18	**52**
Tamarix ramosissima			**21**		14					
Yucca angustissima			5			17	20	14	**24**	10

(con.)

Table 3 (Con.)

Species	CORA	Aband. fields	Riparian	Hang. garden	ARTR	JUOS PIMO	Rock. crev.	Mt. brush	PIPO	PSME ABCO
Monocotyledonus herbs										
Agrostis stolonifera				**28**						
Aristida purpurea	10	**33**	5		14	11	24	2	9	
Bromus ciliatus		17	**37**	20				2		14
B. diandrus		17	**42**					2		
B. rubens	**80**	17				25	12	5	3	
B.tectorum	70	**100**	47		86	54	24	37	33	10
Calamagrostis scopulorum				**79**						
Calochortus flexuosus	**40**					2				
Carex curatorum				**28**						
C. rossii			5	20		13	48	26	42	**57**
Elymus elymoides	20		11		**57**	26	12	14	9	10
Hilaria jamesii	**60**	17			43	22	4	4		
Muhlenbergia thurberi				**33**			32			
Poa bigelovii	**30**					3		2		
P. fendleriana		17	47		14	69	84	74	**85**	71
P. pratensis			**21**			1		7	6	14
Sporobolus cryptandrus	20	**67**	21		29	11	12	26	12	5
Stipa hymenoides	**40**		21	20	29	32	16	19	9	5
Vulpia octoflora	**70**	17	16		43	35	44	14	24	5
Dicotyledonous Herbs										
Antennaria rosulata				**20**		1		2		
Apocynum androsaemifolium				**40**						
Aquilegia chrysantha				**50**						
A. formosa				**50**						
Arabis perennans	20		32			**57**	36	47	36	38
Arenaria fendleri							**64**	7	18	
Artemisia dracunculus		**33**			14	2		11	3	
A. ludoviciana		17	**42**	20		17	12	25	12	14
Aster glaucodes			5	**40**		2		2		
A. herperius				**72**						
Astragalus nuttallianus		**40**				4				
Castilleja scabrida							**60**			
Chaenactis douglasii						18	**36**	12	30	10
Cirsium arizonicum				**26**		3	8	7	9	
Comandra umbellatum						11	16	19	**24**	10
Cryptantha (unknown annual)	**50**				14	32	32	18	12	
C. confertiflora							**36**			
Descurainia pinnata	**40**				29	18		5		5
Dodecatheon pulchellum				**44**						
Draba asprella			16	20		4	32	11	15	**38**
D. verna	**50**		11		14	21	12	9	6	
Eriastrum eremicum	**30**					3				
E. spariflorum	10		5		**29**	7				
Erigeron canaani			5				**28**	4	9	24
E. divergens					**29**	8		5	9	
E. sionis	10					**29**	20	12		5
E. utahensis				**39**						
Eriogonum palmerianum	**50**					8		2		
E. racemosum	10		26	20		16	16	**33**	27	24
Erodium cicutarium	10	**50**			14					
Erysimum asperum			11			27	8	**32**	30	19
Eupatorium herbaceum			21	**40**				2		19
Euphorbia albomarginata	10	**67**	11	20	14	9	4		6	
Gilia inconspicua	**90**		11			49	16	25	12	
Heterotheca villosa		33	37	20	14	14	**64**	32	49	10
Heuchera rubescens			11				8	2		**29**
Lactuca serriola		**50**	16		14	3		4		
Lobelia cardinalis				**56**						
Machaeranthera canescens			5			11	8	**32**	15	5
Mimulus cardinalis			**72**							
Oenothera pallida	**33**					4				
Pectocarya setosa					**29**	1				

(con.)

Table 3 (Con.)

Species	CORA	Aband. fields	Riparian	Hang. garden	ARTR	JUOS PIMO	Rock. crev.	Mt. brush	PIPO	PSME ABCO
Penstemon humilis							**36**			
P. laevis							**40**			
P. rostriflorus			26			7	**28**	18	6	19
Phacelia heterophylla			26	20		8	12	**32**	9	19
Polygonum douglasii						7	12	28	**33**	14
Senecio multilobatus			16	20		36	40	46	**52**	33
S. spartioides			**37**		29	4		14	9	14
Smilacina stellata				**33**						
Solidago sparsiflora			26	**40**		1	28	21	18	19
Stellaria jamesiana			5					18	3	**29**
Sphaeralcea grossularifolia		**33**				5		2		
Stephanomeria tenuifolia			32	20		13	**48**	18	24	19
Streptanthus cordatus	10					**31**		4		10
Thelypodium laxiflorum			**21**			1		4		5
Tragopogon dubius		**67**						4	3	5
Vicia americana			5	20		10		28	12	**48**
Zauchneria latifolia			**26**			1	12	4	6	14
Nonseed plants										
Adiantum capillus-veneris				**89**						
Cystropteris fragilis			**21**	20				2		
Equisetum hyemale		17	**26**	20					3	
No. prevalent species	19	16	22	23	14	22	24	23	22	22
No. modal species	17	12	11	18	8	7	13	4	10	16
No. prevalents encountered	32	25	66	48	32	81	64	83	65	60

for this study. Furthermore, only 117 different species were recognized as prevalent species in the 10 communities of concern (table 3). These data emphasize that most species in the flora of ZNP are uncommon. Only seven species occurred in over 100 macroplots. In order of decreasing commonness, those species are *Poa fendleriana* (189 macroplots), *Amelanchier utahensis, Quercus gambelii, Bromus tectorum, Arabis perennans, Opuntia macrorhiza*, and *Juniperus osteosperma* (115 macroplots). All are native perennials with the exception of *Bromus tectorum,* which is both an annual and an alien to North America. Woody species are over-represented in this group of seven common species, since woody taxa account for only 19.6 percent of the species of occurrence in the full flora of the Park.

The data (table 3) show that only *Bromus tectorum* was a prevalent species in seven plant communities. Another five species were prevalents in six different plant communities. That group of broadly adapted, abundant species consisted of *Amelanchier utahensis, Opuntia macrorhiza, Quercus gambelii, Poa fendleriana*, and *Arabis perennans.*

The vast majority of prevalents (71 species) were so narrowly adapted that they were designated as prevalent species in a single community only. Such data further emphasize that most species are uncommon in any region.

Analysis shows that woody species are significantly more likely to be prevalent (39 of 117 prevalents) than one would expect by chance given the incidence of woodiness in the Park flora (19.6 percent of the 929 taxa). Wind pollinated taxa are also significantly more likely to be prevalents (39 of 117 prevalents) than expected by chance, since only 23.4 percent of the taxa in the flora were considered to be wind pollinated. Alien species were about equally represented in the Park flora (9.8 percent) and among the prevalents (9 taxa) listed in table 3.

In table 4, we present values for four different indices considered to reflect diversity or rarity characteristics inherent in each plant community considered. It is immediately clear that neither the average number of species per macroplot nor the MacArthur-Wilson diversity index show much difference among the 10 plant communities. By both indices, sagebrush and abandoned field communities have the lowest values observed for the 10 communities.

In contrast, both the distinctiveness index and especially the rarity index show large differences among the communities considered (table 4). The distinctiveness index indicates the percentage of prevalents species achieve maximum regional commonness in that community. Three communities show less than 40 percent of their prevalents reaching maximum regional abundance in that community (the mountain brush, ponderosa pine, and juniper-pinyon communities). Other communities such as hanging gardens, blackbrush, and abandoned fields have over 80 percent of their prevalents achieving maximum regional commonness in that community (table 4).

The rarity index shows low values for the juniper-pinyon, mountain brush, ponderosa pine, rock crevice, and Douglas-fir-white fir communities (table 4). Low rarity scores indicate that few of the prevalent species in a community are otherwise rare in the region. Three communities (hanging gardens, sagebrush, and abandoned fields) had very high values for the rarity index. High rarity values arise when many of the commonest species in the community are uncommon in all other communities in the region.

Table 4—Four indices reflective of phytodiversity or species rarity are presented here for the 10 major plant communities of Zion National Park.

	Indices			
Plant community	Average no. species per macroplot	MacArthur-Wilson diversity	Distinctiveness	Rarity
Blackbrush	19	17.4	81	14.4
Abandoned fields	16	14.8	82	29.3
Riparian	22	17.5	60	18.3
Hanging gardens	23	20.8	96	37.2
Sagebrush	14	12.8	53	31.8
Juniper-pinyon	22	19.5	39	4.0
Rock crevices	24	20.9	54	6.8
Mountain brush	23	18.2	17	4.4
Ponderosa pine	22	18.1	38	4.5
Douglas-fir-white fir	22	19.1	60	8.5

Discussion

The prevalent species concept as formulated by Curtis (1959) provides an objective method for identifying the important species of any particular community. Since there are usually more species encountered in large samples of any community than one can list and discuss within the space limitations of a published report, there is a definite need for an objective method for selecting a manageable number of species representative of any community type. By focusing on the commonest species, as the prevalent species concept does, one identifies those species from the regional flora that are best adapted to the unique environments associated with a particular community type. Our experience has demonstrated that one is often unable to identify any behavior characteristic that is statistically over- or under-represented in a given community type relative to the representation of that character in the regional flora, when every species encountered in the community sample is used for the test. However, when such tests are based upon prevalent species, various behavioral traits (such as plant longevity, pollinating agent, or lifeform-class) can be demonstrated to diverge significantly from their commonness in the regional flora. Apparently, species that survive only in rare microsites within a community or that represent chance introductions that will not long survive in the community weaken analyses based upon all species encountered in a sample.

The foregoing discussion illustrates the desirability of simultaneously studying the entire flora and the full vegetational complex of an area. Without a regional checklist of species occurring in a region, one cannot determine whether any particular plant characteristic is being selected for or against in a particular environmental complex. However, when both a regional checklist and prevalent species list exists for a particular community types in that region, it is possible to use Chi-square tests to determine whether a given plant character is over- or under-represented in a particular community. In ZNP, for example, the checklist shows that 236 of the 929 species in the Park are annuals or biennials. In the lowest elevation and driest plant community (blackbrush), 10 of 19 prevalent species are annuals. A Chi-square test suggests that the annual habit is significantly over-represented in the blackbrush community, given the incidence of annuals in the regional flora (SX^2 value = 10.4, $p < 0.01$). By contrast, annuals are significantly less common than one would expect by chance (none of the 22 prevalents are annuals) in the Douglas-fir-white fir community, the highest elevation community in ZNP (SX^2 value = 7.4, $p < 0.01$).

Although Curtis (1959) made no inferences about genetic variability and modal species, we suggest that modal species are likely to harbor more genetic diversity than non-modal species in the community of modality. We draw that inference from the fact that the origin of new mutations is directly proportional to the size of a population (Dobzhansky 1951). In addition, as Wright (1931) theorized, the rate of gene loss by "drift" from a population is inversely proportional to population size. Consequently, we suggest that genetic diversity should be greatest for a species where it is modal (regionally most common). Furthermore, those communities in which a large percentage of the prevalents are also modal (that is, community distinctiveness is high) are likely to harbor more genetic diversity (summed across all constituent species) than communities having low distinctiveness indices (see table 1 for definitions). Again, Curtis (1959) makes no connection between community distinctiveness and genetic diversity inherent in a community, but we suggest that such a correlation is likely.

The rarity index varies in magnitude according to the degree to which species common (prevalent) in one community are uncommon in other communities of the region. Since rarity is of unusual interest to many users of plant communities, managers would benefit from an index that objectively quantified the amount of rarity in communities. The rarity index of table 1 provides a means for ranking local communities in respect to the degree to which they harbor species that are elsewhere uncommon in the region. Since the index is based on prevalent species, it also identifies those communities in which regionally uncommon species maintain larger populations and are likely to generate and conserve genetic diversity important for their continued persistence in the region.

Finally, we acknowledge that the distinctiveness and the rarity indices are positively correlated, but their relationship is sufficiently diffuse that we recommend that both be used to describe plant communities. In respect to distinctiveness for example, the sagebrush community ranked seventh from the top, but by the rarity index, sagebrush communities rank second from the top. Both indices provide information useful to managers, and since their values sometimes differ markedly for the same community, we recommend that both be used to describe communities.

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