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Sierra Nevada Meadows: Species Alpha Diversity

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Plant species diversity refers to variety and abundance; it does not necessarily relate to meadow health but may provide information important in an ecosystem context. Monitoring to detect change in diversity usually begins with estimating alpha (within) diversity of plant communities. Because few such estimates exist for meadow site classes or specific sites of the Sierra Nevada, California, we computed Margalef's diversity index (D_m), which stresses species richness, and Simpson's index (D_s), which stresses species dominance, for two sets of frequency data. Frequency was estimated by the nearest shoot-to-point method and the rooted quadrat method. In addition, a relative index (D_r) was calculated on the basis of the number of species on individual sites divided by the average number of species recorded for 107 meadow sites. Regardless of the data set or index, species diversity was lower for sites at or near the environmental extremes of moisture. The methods used to estimate frequency, estimating species numbers, and the value of diversity estimates are discussed.

Retrieval Terms: Relative index, Margalef's index, Simpson's index, jack-knife estimates, plant species, frequency

Meadows are the most biologically active of the plant community types of the Sierra Nevada, California. They contribute a high proportion of the forage for many forest grazing allotments, park preserves, and wilderness areas. They supply habitats for wildlife populations. By providing scenic vistas, the meadows' timbered edges are favored campsites of forest, park, and wilderness visitors. The meadows also help to filter sediments from water from surrounding slopes, thereby assuring clean streams and lakes. These characteristics indicate that the meadows of the Sierra Nevada possess high biological diversity.

Biological diversity refers to variety and abundance; it involves ecological processes, structures, and functions and may occur at any spatial scale;[1] it is variety or multiformity—of different forms or kinds.[2] Included under the biological umbrella are genetic, species, structural, and landscape diversities.

Furthermore, there are alpha (within), beta (between), and gamma (large scale) diversities.[3] Alpha diversity is represented by a plant community, the populations co-occurring at a specific time in a specific space.[4] Beta diversity is represented by differences between communities present along a gradient (e.g., topography, soil acidity, or moisture regime) or the same place over time. Gamma diversity is represented by the kinds of plant communities present or the total number of species present in a specific geographic area (e.g., meadow system or watershed).

Diversity has two components, richness and evenness.[5,6] Richness refers to the number (variety) of different kinds of things (species, for example), while evenness refers to the equality of the kinds of things (abundance or numbers, for example).

A key to the high biological activity, hence diversity, of meadows is the mix of plant communities represented by individual sites. Meadow sites are defined as areas of homogeneous species composition that have a general species composition visually different from that of adjacent areas.[7] The plant species present may be the same, but their proportions of the vegetation will be visually different on different sites. Meadow site classes are composed of sites with the same dominant species and similar composition.

Climax plant communities are often thought to possess higher diversity than seral communities. But within specific sites, physical/chemical factors or intense competition, or both, may work to reduce diversity.[8] Also, gamma diversity will likely be higher when the communities of an area are in different stages of a sere than when they are all in the same stage.

Increasingly, land managers are asked to monitor and estimate change in diversity. In order to derive the greatest benefit from monitoring efforts, managers need to know how to interpret high versus low diversity within and among different plant communities. Monitoring diversity will usually begin with an estimate of alpha diversity. Nevertheless, now such estimates are rare for meadows of the Sierra Nevada.

The objective of this paper, therefore, is to provide land managers indices of plant community **alpha diversity** to serve as guides to indices that can be expected given similar vegetation. Two sets of diversity indices are given: (1) average diversities for meadow site classes and (2) average diversities for individual sites.[9,10]

METHODS

Data

Data from 82 meadow sites in 14 meadow site classes (Stanislaus National Forest to the Sequoia National Forest) were used.[7] The data from each site constituted a list of the plant species found (except trees) and their nearest shoot-to-point frequencies. Species lists were derived from thorough searches of the sites before and during sampling. Frequencies were calculated from a sample of 300 points per site.

A second set of data came from two meadows in Yosemite National Park.[10] Rooted frequency (presence) was recorded for the species on 12 sites in the meadows, using 100 randomly located quadrats per site. For purposes of this study, the quadrats from each site were randomized into 10 samples of 10. For sampling rooted frequency, the quadrat size used (10 cm × 10 cm) was found appropriate on dry meadows in Idaho and is used on meadows of the Pacific Southwest Region of the Forest Service.[11,12]

Diversity Indices

Two common indices of diversity were used: (1) Margalef's $\{D_m = (S - 1)/\ln N\}$, where S is the number of species and N is the total number of individuals (hits or occurrences) for all species; (2) Simpson's $\{D_s = 1/D\}$,

$$\text{where } D = \sum_{i=1}^{S} (n_i(n_i - 1)/N(N - 1))$$

and n_i is the number of individuals of the *i*th species.[6] These indices were selected because they do not require testing assumptions regarding the underlying species abundance distributions. In addition, D_m was selected for its simplicity and because it stresses the species richness component. D_s was selected because it is well known and stresses the species evenness (dominance) component.

In addition, a relative index ($D_{ri} = s_i/Ss$) was used, where s_i is the number of species found on a specific site (i) and Ss is a standard number of species. This simple index was used to avoid problems such as variation in sampling techniques. It is a measure of species richness relative to the standard.

Analyses

A guiding motive was to provide managers estimates of alpha diversity that could be compared with estimates found on meadow sites with similar vegetation. Direct comparison of different indices for estimating alpha diversity was not intended.

D_r, D_m, and D_s were calculated for each of 82 sites.[7] Average diversity was calculated for all 82 sites and for each of 14 meadow site classes *(table 1)*.[7,9] Within-class variances were estimated but not used; the numbers of sites were generally few and did not constitute a random sample.

Species totals for all 100 quadrats were used to compute the three diversity indices for each of the 12 sites in Yosemite.[10] Jack-knife diversity estimates and pseudovalues were then computed by deleting, in turn, each random sample of ten quadrats. Pseudovalues from the jack-knife procedure are asymptotically normally distributed, their mean is the best estimate of diversity, and the "t" distribution may be used to compute confidence intervals.[6] Therefore, from the pseudovalues, the average and standard error of each diversity index were derived for each site.

In all cases, the value of Ss used to compute D_r was the average of the s_i from 107 sites sampled over a 10-year period (1973 to 1983). As above, the sites were not a random sample of meadow sites of

Table 1—*Class names, numbers of sites sampled (N), average numbers of species (Sp), percent composition of the most frequent species (Comp), and means of three indices of species diversity for 14 meadow site classes in the Sierra Nevada, California.*

Meadow Class[2]	N	Sp	Comp[3]	Diversity index[1] D_r	D_m	D_s
			pct			
Hypericum/Polygonum/Viola (hillside bog)	19	29.6	9.4	1.396	3.691	8.888
Trifolium/Mimulus (carpet clover)	4	28.8	19.7	1.357	3.375	8.010
Agrostis (bentgrass)	2	20.0	22.3	0.944	3.068	7.836
Deschampsia/Aster (tufted hairgrass)	6	22.5	14.2	1.062	2.659	7.986
Poa (Kentucky bluegrass)	3	21.0	48.3	0.991	2.630	4.021
Muhlenbergia/Heleocharis (pullup muhly)	8	23.0	21.9	1.086	2.542	6.665
Heleocharis/Muhlenbergia (fewflowered spikerush)	8	20.4	33.8	0.962	2.476	5.766
Calamagrostis/Oryzopsis (shorthair)	8	18.5	39.3	0.873	2.389	4.560
Trifolium/Muhlenbergia (longstalk clover)	4	20.0	23.6	0.944	2.279	6.241
Gentiana/Aster (gentian-aster)	3	19.3	13.1	0.912	2.104	5.947
Carex nebraskensis (Nebraska sedge)	5	18.8	38.2	0.887	1.893	3.837
Heleocharis/Heleocharis (ephemeral-lake)	2	8.5	58.7	0.402	1.052	2.391
Carex exserta (shorthair sedge)	4	10.5	86.0	0.496	0.964	1.404
Carex rostrata (beaked sedge)	6	9.0	78.5	0.425	0.906	2.494
Overall average diversity	82			1.010	2.551	6.096

[1] D_r = relative index of diversity; D_m = Margalef's index of diversity; D_s = Simpson's index of diversity.

[2] As defined by Ratliff[9] and ordered from highest to lowest diversity by D_m.

[3] Nearest shoot-to-point composition.[9]

the Sierra Nevada. Nevertheless, they cover the range in species numbers that may reasonably be expected. Therefore, Ss = 21.187, and (as a best estimate) the 95 percent confidence interval for the true value was 19.621 to 22.753 species.

RESULTS

Class Alpha Diversity

What diversity values may one expect to find for different kinds of meadow?

Hillside bog meadows exhibited the highest plant species diversity regardless of the index used *(table 1)*. Such sites occur on slopes and have "hanging" hydrologic regimes defined by constant watering by flows from springs and seeps.[13]

Meadow site classes, representing the environmental extremes, had the lowest diversities, regardless of the index, but each index was lowest on a different class. Full agreement was not expected because D_m and D_s stress different components of diversity and are not significantly correlated.[6] Furthermore, D_r depended on the total number of species found, whereas D_m depended on the number of species encountered during sampling. D_r was lowest on ephemeral lake sites, where the "sunken concave" hydrology is defined by seasonally ponded water that is recharged by flows from upstream.[13] D_m was lowest on *Carex rostrata* (beaked sedge) sites. These sites have "lotic" hydrology, defined by moving surface water that is constantly recharged by flows from upstream. D_s was lowest on *C. exserta* (shorthair sedge) sites, which occur on slopes or benches. These sites have "xeric" hydrology, defined by being recharged seasonally by precipitation and becoming quite dry during summer.

Most sites of the meadow classes whose diversity indices straddle the overall averages have "normal" hydrologic regimes. Normal hydrology is characteristic of sites that obtain water from the water table, are recharged by precipitation, and may dry in the surface during summer.[13]

Deviations from the overall averages were greater for the least diverse classes than for the most diverse one, probably reflecting proportions of the different classes in the sample. For each index, 23 percent of the sample sites were in the class with the highest diversity, while the greatest proportion of sample sites in classes with the lowest diversities was 7.3 percent. For D_r, D_m, and D_s, respectively, the highest diversities were 38.2 percent, 44.7 percent, and 45.8 percent more than and the lowest diversities were 60.2 percent, 64.5 percent, 77.0 percent less than the overall averages. This finding points out the need for stratified random sampling when estimating the gamma diversity of a meadow, allotment, or watershed.

Site Alpha Diversity

What diversity values may one expect to find on specific sites?

Dividing the quadrats on a site into 10 samples probably reduced their value for estimating frequency. Nevertheless, doing so provided a way to estimate the means of diversity indices and their standard errors *(table 2)*. In turn, that permitted the 95 percent confidence intervals to be computed. Site number 3, for example, had the highest frequency of *Carex nebraskensis* (Nebraska sedge) and *Aster alpigenus* (alpine aster) *(table 3)*. The 95 percent confidence intervals for that site (with 9 degrees of freedom) for D_r, D_m, and D_s were $0.703 < D_r < 0.896$, $1.822 < D_m < 2.474$, and $8.374 < D_s < 9.302$. Similar intervals may be computed for the other sites, and by using the rooted frequency method and the same size quadrats, similar sites should have diversities within, or at least near, those intervals.

Because different methods of estimating frequency were used, direct comparisons of the D_m's and D_s's for the two data sets could not be made. They nevertheless supported each other. Ordination of the Yosemite sites approximated a moisture gradient.[10] The lowest diversities occurred at or near either end of this gradient *(table 2)* and thereby displayed the influence of environmental extremes. Diversity was higher at the wet end of the gradient than at the dry end, but diversity was clearly highest on sites with medium moisture. Although diversity of the wettest of the

Table 2—*Three indices of plant species diversity on 12 meadow sites in the Sierra Nevada, Yosemite National Park, California (based on species present in 100, 10-cm by 10-cm quadrats).*

		Diversity index					
		Relative		Margalef's		Simpson's	
Site[1]	N[2]	Mean[3]	SE[4]	Mean	SE	Mean	SE
4	16	0.925	0.130	2.672	0.459	7.064	0.218
3	16	0.798	0.042	2.148	0.144	8.838	0.205
5	31	1.761	0.111	4.950	0.375	13.915	0.428
2b	22	1.208	0.069	3.345	0.235	11.988	0.349
2a	19	0.982	0.057	2.663	0.194	9.318	0.209
6b	19	1.109	0.071	3.110	0.241	8.093	0.121
6a	21	1.076	0.057	3.014	0.199	7.916	0.300
1	31	1.633	0.094	4.592	0.319	12.282	0.399
7	18	0.892	0.042	2.570	0.158	7.369	0.297
8	25	1.307	0.091	3.612	0.304	10.423	0.405
9a	15	0.878	0.069	2.644	0.260	5.877	0.196
9b	13	0.656	0.042	1.932	0.153	4.462	0.247

[1] Site order approximates a decreasing soil moisture gradient (top to bottom); letters are site subdivisons.[10]
[2] N = number of species on the site.
[3] Jack-knife mean diversity based on 10 samples of 10 quadrats each.
[4] Standard error of the jack-knife mean.

Table 3—*Rooted frequencies (percent) of 21 species on 12 meadow sites, Yosemite National Park, 1983.*

	Site[1]											
Species	4	3	5	2b	2a	6b	6a	1	7	8	9a	9b
Phalacroseris bolanderi	97	79	42	6								
Carex rostrata	5	31	21									
Deschampsia caespitosa	1	16	66	24		3	1					
Carex nebraskensis	23	54	1	43	36	3	8					
Aster alpigenus	56	73	63	56	33			14				
Juncus orthophyllus	25	46	12			1	3	9				
Heleocharis pauciflora	100	95	40	94	98	96	89	2	2			
Mimulus primuloides	30		68		3	28	7			5		
Juncus balticus	1	2		27	7	6	42	16				
Perideridia bolanderi	43	77	32	84	82	66	70	11	26	55	3	
Muhlenbergia filiformis	32	64	46	57	42	59	38	40	50	89	15	15
Hypericum anagalloides		5	36	4	2	27	4	2				
Trifolium longipes			19	26	99	88	23	75	12			
Danthonia californica			13	35	80	91	80	11	48	22	1	
Aster occidentalis			6	19	58	93	90	92	94	2	12	
Penstemon rydbergii						2	11	26	46	6	89	63
Stipa columbiana								32	26		1	7
Horkelia fusca								28	1		51	97
Agrostis idahoensis									17	22	28	6
Polygonum douglasii									10	22	57	14
Lupinus confertus									6	5	61	56

[1] Site order approximates a soil moisture gradient; letters are site subdivisons.[10]

12 sites appears greater than that of the wettest of the 82, beaked sedge and ephemeral lake sites were not among those studied in Yosemite.

D_r values are directly comparable, because only numbers of species are involved and the index is based on a standard. Again, sites at the extremes of the moisture gradient tended to have lower diversity than those near the middle.

DISCUSSION

Frequency Estimates

Although both methods of estimating relative abundance by frequency appear to reflect species diversity adequately, they have shortcomings.

With the quadrat method two equally frequent species may differ considerably in actual abundance. For example, one may be represented by many shoots, whereas the other may be represented by relatively few shoots but be equally well distributed and occur in the same number of quadrats. In order to avoid that problem, the use of a large number of very small quadrats is suggested for estimating abundance.[6]

Especially where quadrats of a single size are used, managers may have to accept that some frequencies will be too large and some too small to be of much value in assessing beta diversity over time. The 10-cm by 10-cm quadrat used in Yosemite may be too large even on dry meadows in the Sierra Nevada. A quadrat of appropriate size will give a frequency of between 63 percent and 86 percent for the most abundant species.[14] For the sites in Yosemite (except number 5), frequencies for the most abundant species exceeded that range *(table 3)*. Thirty-nine percent of the species frequencies were above the minimum of 20 percent suggested for detecting change in the less abundant species.[15]

A point is a dimensionless (in practice a very small) quadrat, and direct hits on species (as with sampling pins) may be used to estimate their relative abundances.[6] In situations where one encounters grazed and ungrazed meadows, point hits on foliage can give misleading results. For that reason, basal point hits have been used, but even in meadows, actual basal hits on plants are rare. For example, only 4.4 percent of all basal hits on 82 sites were on plants (excluding mosses).[7]

The nearest shoot-to-point method does not estimate percent ground cover. Nevertheless, for estimating diversity, that method appears to fit the need for large numbers of small quadrats and to reflect relative species abundances in meadows adequately. A point is the center of a circular quadrat of variable size, but I consider the average shoot-to-point distance in meadows to be short enough to justify accepting the nearest shoot to the point as being hit. The average distance from 4,766 random points to the centers of the nearest shoots was 5.902 ± 0.163 mm (a circular quadrat of 1.1- to 1.2-cm diameter).[16] The method estimates the relative probability of finding a given species at a random point and hence relative species frequency.

Nevertheless, because of the variable quadrat size and the likelihood of nonrandom shoot dispersion, the nearest shoot-to-point method of estimating the proportions of shoots by species is not statistically acceptable. Therefore, statistical inferences regarding individual species should be avoided. For that purpose, rooted frequency in quadrats of fixed size should be preferred.

Species Numbers

Estimating the number of species on a site appears to be a simple approach to diversity. The most prevalent species usually will be immediately obvious to the observer. Nevertheless, the more time spent in observation, the more species one will find. For example, different species may appear under different conditions, and several periods of observation may be needed to be sure most species have been recorded. An alternative approach may be to record only those species found within a specified observation time, say 45 minutes, at a time when an indicator species reaches a selected phenologic stage.

Why Assess Diversity?

Indices of alpha diversity appear to be of little management value in and of themselves. Diversity indices do not necessarily relate to ecological state or meadow health. These characteristics may be better related to the basic measures of species cover, composition, and biomass production. Nevertheless, plant species diversity is important as related to processes and flow pathways within and among communities. Higher diversity implies a greater number of occupied niches.[3] Over the growing period, plant species vary in their ability to capture the sun's energy, and a high degree of diversity in the plant community may equate with high diversity in other parts of the biotic system. For example, with several co-dominant rather than one dominant grass species, the diversity of decomposer organisms may be higher, thereby affecting nutrient cycling rates. Herbivore diversity may be higher with many different herbaceous species than with few, thereby affecting herbage use.

Thus, when considered in an ecosystem context, alpha diversity indices provide information that may not be immediately apparent from basic measures of the plant community.

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