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MULTISCALE SAMPLING OF PLANT DIVERSITY: EFFECTS OF MINIMUM MAPPING UNIT SIZE

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Abstract. Only a small portion of any landscape can be sampled for vascular plant diversity because of constraints of cost (salaries, travel time between sites, etc.). Often, the investigator decides to reduce the cost of creating a vegetation map by increasing the minimum mapping unit (MMU), and/or by reducing the number of vegetation classes to be considered. Questions arise about what information is sacrificed when map resolution is decreased. We compared plant diversity patterns from vegetation maps made with 100-ha, 50-ha, 2-ha, and 0.02-ha MMUs in a 754-ha study area in Rocky Mountain National Park, Colorado, United States, using four 0.025-ha and 21 0.1-ha multiscale vegetation plots. We developed and tested species–log(area) curves, correcting the curves for within-vegetation type heterogeneity with Jaccard's coefficients. Total species richness in the study area was estimated from vegetation maps at each resolution (MMU), based on the corrected species–area curves, total area of the vegetation type, and species overlap among vegetation types. With the 0.02-ha MMU, six vegetation types were recovered, resulting in an estimated 552 species (95% CI = 520–583 species) in the 754-ha study area (330 plant species were observed in the 25 plots). With the 2-ha MMU, five vegetation types were recognized, resulting in an estimated 473 species for the study area. With the 50-ha MMU, 439 plant species were estimated for the four vegetation types recognized in the study area. With the 100-ha MMU, only three vegetation types were recognized, resulting in an estimated 341 plant species for the study area. Locally rare species and keystone ecosystems (areas of high or unique plant diversity) were missed at the 2-ha, 50-ha, and 100-ha scales. To evaluate the effects of minimum mapping unit size requires: (1) an initial stratification of homogeneous, heterogeneous, and rare habitat types; and (2) an evaluation of within-type and between-type heterogeneity generated by environmental gradients and other factors. We suggest that at least some portions of vegetation maps created at a coarser level of resolution be validated at a higher level of resolution.

Key words: Jaccard's coefficients; keystone ecosystems; minimum mapping unit; modified-Whittaker plot; species–area curves; species overlap; vascular plant diversity.

INTRODUCTION

The patterns and theories of biological diversity provide a sound, scientific basis for the study and management of natural resources (Huston 1994). Three potential scales of study for biological diversity are: coarse scale (typically 100-ha minimum mapping unit, MMU), landscape scale (typically 2-ha to 100-ha MMU), and fine scale (<2-ha MMU, such as 30 × 30 m pixels or smaller). Disproportionate numbers of studies have been conducted at the two extremes. There are active research programs, for example, to quantify patterns of biological diversity at coarse scales (Austin and Heyligers 1991, Messer et al. 1991, Palmer et al. 1991, Stoms 1992, Scott et al. 1993). Also, many plant studies are conducted with plot sizes <3 m^2, with fewer than five replicates (Kareiva and Anderson 1988).

Ecologists are struggling to develop strategies to quantify the biological diversity of landscapes and regions (e.g., Margurran 1988, Wilson 1988, Soulé and Kohm 1989, Peters and Lovejoy 1992, Noss and Cooperrider 1994) and to link vegetation analyses across scales (Franklin 1993, Short and Hestbeck 1995). Plant species lists for most National Parks are obtained from decades of searching and cataloging, with no statistical way to determine the completeness of the lists or to examine them spatially (Stohlgren et al. 1995*b*). In the Rocky Mountains of Colorado, conservationists and resource managers require detailed information at multiple scales to evaluate, for example, invasions of nonnative plant species and the effects of elk on plant diversity, and to protect highly diverse or unique habitats. Riparian zones (Baker 1990) and aspen stands (Peet 1981), for instance, are known to have high plant diversity. However, attempts to quantify the relative contributions of various plant communities to the total plant diversity of large areas remain hampered by poor multiple-scale vegetation sampling methods. To accomplish this linkage from plots to landscapes, much more work is needed on: (1) multiscale field techniques

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to assess plant diversity; (2) mathematical models to estimate the number of species in larger areas; and (3) evaluation of the ecological costs and benefits of sampling at alternative scales, relative to the economic costs.

Since costs constrain the portion of a landscape that can be sampled, researchers often reduce the number of vegetation classes considered and/or increase the MMU (decreasing the resolution). Ecologists rarely know how such decisions affect the accuracy and completeness of information on plant diversity maps.

There are two types of "gaps" created with traditional methods that decrease map resolution. The first type occurs when a resource is recognized as unprotected because it is not in a protected area, such as a national park or state refuge (Scott et al. 1993). A second type of gap occurs when a resource inside or outside a protected area remains undetected (or undervalued) because of the scale and resolution of the data. We are concerned with the second case. For example, present models of plant species distributions have performed poorly for rare species because data usually are not available from certain cover types occupying small areas (Cherrill et al. 1995). In our area, aspen (*Populus tremuloides*) occupies <2% of the forested landscape in the Front Range of the Colorado Rockies, often in small patches (Peet 1981, 1988). Vegetation maps created with minimum mapping units 2 ha or larger may grossly underestimate aspen cover. Not knowing the actual cover of aspen forests translates into a gap in the knowledge needed to manage this rare habitat that is valuable for many wildlife and plant species (Salt 1957, DeByle 1985, Mueggler 1985) and for fire prevention (Jones and DeByle 1985).

It is becoming increasingly important for sampling strategies to quantify patterns of plant diversity at multiple spatial scales and to detect rare and important habitats (Stoms 1992, Colwell and Coddington 1994). A survey strategy should be tailored to describe resources and to answer management questions at appropriate spatial scales. Conversely, it should be recognized that resource information collected at one scale may be totally inappropriate for addressing questions at another scale. A problem arises when management decisions are made based on the "best available" information if the completeness, accuracy, and scale of the information have not been evaluated thoroughly. To evaluate patterns of plant diversity at landscape scales, information is needed on species diversity within vegetation types, species–area relationships, and species diversity between types. This information can then be used to estimate total plant species richness in an area and to assess the effect of minimum mapping units on estimates of plant diversity, with a minimal amount of field sampling.

We used: (1) stratified random sampling of vegetation communities based on interpretation of aerial photography; (2) multiscale vegetation sampling techniques to assess plant diversity (species richness, and species composition overlap within and among communities); and (3) geographic information system (GIS) and mathematical techniques to compare plant diversity patterns resulting from various minimum mapping units.

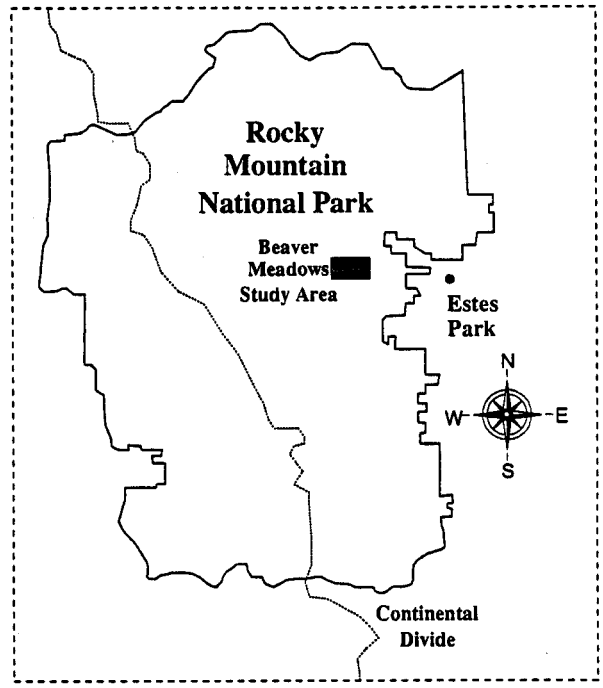

FIG. 1. Location of the Beaver Meadows study area in Rocky Mountain National Park, Colorado, USA.

STUDY AREA AND METHODS

The Front Range of the Rocky Mountains in Colorado ranges in elevation from 1600 m to nearly 4350 m, and contains a variety of vegetation communities from prairie to alpine tundra. Dominant types and species (generally from low to high elevations) include: prairie vegetation dominated by short grasses (*Bouteloua gracilis, Buchloe dactyloides*) and sage brush (*Artemisia tridentata*); ponderosa pine (*Pinus ponderosa*); Douglas-fir (*Pseudotsuga menziesii*); lodgepole pine (*Pinus contorta*); aspen (*Populus tremuloides*); limber pine (*Pinus flexilis*); and spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Peet 1988). Our study site was a 754-ha area (2500–3000 m elevation) in the Beaver Meadows area of Rocky Mountain National Park (Fig. 1).

Using 1:15 840 natural color aerial photographs taken 28 September 1987, we stratified the vegetation to include lodgepole pine, ponderosa pine, wet meadow (dominated by *Poa palustris, Deschampsia caespitosa,* and *Poa interior*), dry meadow (dominated by *Carex helianthus* and *Artemisia tridentata*), and aspen communities. The ponderosa pine community was further stratified into burned (prescribed fire in September 1994) and unburned ponderosa pine. We had a mini-

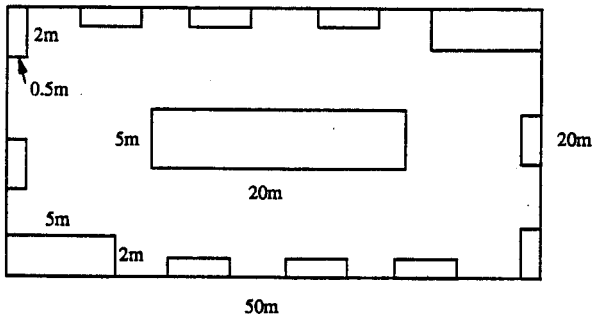

FIG. 2. The modified-Whittaker nested vegetation plot.

mum mapping unit of 0.02 ha. We overlaid a 48 × 32 unit grid (north to south) over the aerial photograph and randomly selected (using a computer random number generator) five to seven potential sample points in each of the six plant communities. We located the points in the field with the aid of the photographs, other maps, and a compass, and later checked and mapped the locations with a global positioning system (GPS; Trimbal Pathfinder Professional, Trimble Navigation Limited, 645 North Mary Avenue, Sunnyvale, California 94086 USA.). For each field site, we calculated slope, aspect, and elevation (using digital elevation models and our GPS information). At each point, we established a modified-Whittaker nested vegetation sampling plot (Stohlgren et al. 1995*a*).

Multiple-scale vegetation sampling

The modified-Whittaker plot (Fig. 2) is 20 × 50 m, with 10 0.5 × 2 m (1-m^2) subplots arranged systematically inside and adjacent to the plot perimeter, two 2 × 5 m (10-m^2) subplots in opposite corners, and a 5 × 20 m (100-m^2) subplot in plot center. Cumulative species (additional species found in the subplot or plot) are recorded successively in the 10 1-m^2 subplots, the two 10-m^2 subplots, the 100-m^2 subplot, and the remaining unsampled areas of the 20 × 50 m plot. For the small, burned ponderosa pine vegetation type, the dimensions of all the subplots and plots were halved. Those species unique to a particular vegetation type, which were likely to be the species of most conservation interest, were also noted. We used a global positioning system to document the locations of the plots and to incorporate the data directly into our geographic information system (GIS).

Determining the appropriate species–area curve model

Cumulative species data from the 1-m^2, 10-m^2, and 100-m^2 subplots from each 1000-m^2 plot were fit to species–log(area) curves and log(species)–log(area) curves after initial tests on subsets of the data showed that these models produced similar, high coefficients of determination (generally, $r^2 > 0.95$), whereas direct species–area curves fit the data poorly. We estimated the total number of species in each 1000-m^2 plot based on the 1-m^2, 10-m^2, and 100-m^2 data and the two regression models. We then compared the estimate to the number of species actually recorded for the 1000-m^2 plot. The species–log(area) model was selected over the log(species)–log(area) model because: (1) the former produced the lowest mean difference in estimated and observed values when using the 1-m^2, 10-m^2, and 100-m^2 subplot data (4.76 ± 0.90 species; mean ± 1 SE, compared to 5.05 ± 0.88 species) and when using the 1000-m^2 data (1.43 ± 0.27 species compared to 1.56 ± 0.28 species); and (2) the log(species)–log(area) curve tended to greatly overestimate species in the most species-rich areas, which would not provide a conservative estimate of species richness. This semilog relationship is reported to be a robust species–area "curve" (Shmida 1984, Stohlgren et al. 1995*a*).

We recognize that the validation of multiscale vegetation sampling methods involves the use of resampled plot data. Earlier nested quadrat designs, such as the nested block design (Mueller-Dombois and Ellenberg 1974; see Stohlgren et al. 1995 for a review), used 50% resampled data, and the original Whittaker design used 20–50% resampled data (in the 1-m^2, 10-m^2, and 100-m^2 subplots). We greatly reduce the use of resampled data with the modified-Whittaker design, which has no overlap in the 1-m^2, 10-m^2, and 100-m^2 subplots, and thus only 13% overlap (resampled data) in the 1000-m^2 plot. That is, "expected" values of species richness in 4000 m^2 of a given vegetation type are derived from sampling 520 m^2 (4 plots × 130 m^2/plot; 10 1-m^2 subplots, two 10-m^2 subplots, and one 100-m^2 subplot per plot).

Correcting the species–log(area) curves for within vegetation-type heterogeneity

Because replicate vegetation plots rarely (never?) have identical species compositions, the average species–log(area) curve (hereafter, simply called species–area curve) would underestimate species richness in replicate plots. Species–area curves based on replicate plots must be corrected for within-vegetation-type heterogeneity. Thus, we developed average species–area curves for each vegetation type and then used Jaccard's coefficient to correct the slope of the average species–area curve (Fig. 3). Jaccard's coefficient accounts for the overlap between two complete species lists (Krebs 1989). Jaccard's coefficient (J) is defined as:

$$J = A/(A + B + C)$$

where A is the number of species found in both paired sites, B is the number of species in site 1 but not in site 2, and C is the number of species in site 2 but not in site 1. In other words, Jaccard's coefficient is the proportion of the two sites' combined diversity that is shared. A comparison of species lists for two sites resulting in a similarity coefficient of 1.0 would indicate complete overlap (i.e., identical species lists), whereas a value of 0.0 would indicate no overlap. We calculated

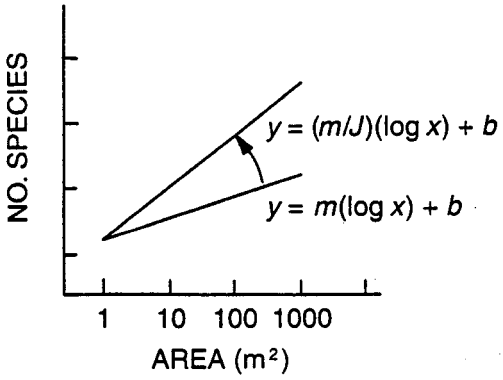

FIG. 3. Species–area curve correction with Jaccard's coefficient. Note the log scale of the x-axis.

the average Jaccard's coefficient for each vegetation type from pairwise comparisons between plots. Mean Jaccard's coefficients were calculated from $n = 3$ J values for three plots, $n = 6$ J values for four plots, and $n = 10$ values for five plots.

The number of species per total area sampled (i.e., the total area of three, four, or five 1000-m² plots) for each community was estimated based on the semilog relationship of the average number of species recorded in 1-m², 10-m², and 100-m² subplots as:

$$y = m(\log x) + b$$

where y is the number of species, x is the combined plot area, b is the constant, and m is the slope. We corrected the species–area curves for within-type heterogeneity by dividing the slope (m) with the average pairwise Jaccard's coefficient ($y = (m/J)(\log x) + b$) for the vegetation type.

We validated the estimates from the corrected species–area curves by using observed values from 1-m², 10-m², and 100-m² subplots to predict the number of species found in the total sampled area of each type (i.e., 3000–5000 m²). We also calculated Jaccard's coefficient for the 1000-m² plot data to further refine the average Jaccard's coefficient and to improve the accuracy of the species–area curves for each vegetation type. The 95% confidence limits of the estimated species richness for each vegetation type were calculated with the standard error of the estimate (y) from the average species–area curve regression (Zar 1974).

Estimating the total number of plant species

To estimate the number of plant species that occur in the 754-ha study area, we first estimated the total number of species found in each vegetation type using species–area curves corrected with Jaccard's coefficient (J). Second, we compared the two types with the highest numbers of species and unique-to-type species. Species lists in these two types overlapped by some percentage (J). Thus, when we composited the first two vegetation types, we corrected the total number of species within the composite by summing the two types and then subtracting J% of the composited species list. Third, we compared the composited type with the next most species-rich type, again correcting for species overlap. These steps were repeated until all vegetation types were combined.

Evaluating the effects of the MMU

After digitizing the high-resolution (0.02-ha MMU) vegetation map from the aerial photography, we used the ELIMINATE command (with KEEPEDGE option; Arc/Info version 6.0, ESRI, 380 New York Street, Redlands, California 92373-9870 USA) to create vegetation maps with minimum mapping units of 2 ha, 50 ha, and 100 ha. For the 50-ha and 100-ha MMU maps, we used the DISSOLVE command to remove polygons less than the MMU and to maintain homogeneity within the combined polygons. For each map, we calculated the area and number of polygons in each of the recognized vegetation types (STATISTICS command). Finally, we estimated the number of species based on the species–area curves for those types (again, correcting for species overlap between vegetation types).

RESULTS

We recorded 330 plant species in the 25 plots sampled (four 0.025-ha plots and 21 0.1-ha plots). By stratifying the vegetation into both large, homogeneous types (e.g., lodgepole pine, ponderosa pine, and dry meadow) and potentially important small-area types (e.g., aspen, wet meadow, and burned ponderosa pine; Stohlgren et al. 1996), and by using unbiased plot locations, we accounted for about one-third of the plant species listed for Rocky Mountain National Park in just 2.2 ha of sampling area.

Species overlap within vegetation types

Species overlap between the replicate plots within a vegetation type ranged from 0.199 in the wet meadow and lodgepole types (i.e., a mean of 19.9% overlap among pairwise comparisons of species lists, J_{1000} used) to 0.318 in the burned ponderosa type (Table 1). Jaccard's coefficient values generally increased slightly when species lists were tested with the 1000-m² plot data (J_{1000}) compared to the 100-m² plot data (J_{100}). The low standard errors of the mean suggest that species overlap was fairly consistent within all types. Higher than average variation in the mean Jaccard's coefficient, or higher than average variation in the slopes or constants in the species–area curves within vegetation types signaled the need to increase the sample size from four to five plots. When additional plots were added in the wet meadow and ponderosa types, the mean Jaccard's coefficient tended to stabilize and the variance decreased. The Jaccard's coefficient was stabilized and the variance was decreased for the dry meadow type by accounting for spatial autocorrelation. This was important because the corrections to the species–area curves are dependent on accurate J values (Fig. 3).

TABLE 1. Mean and SE of Jaccard's coefficient (J_{100}) within vegetation types in the Rocky Mountain National Park, based on 1-m², 10-m², and 100-m² subplots, or all subplots and the 1000-m² plot (J_{1000}), based on $n = 3$, $n = 4$, or $n = 5$ plots.

	Jaccard's coefficients			
	J_{100}		J_{1000}	
Vegetation type	Mean	1 SE	Mean	1 SE
Aspen	0.228	0.021	0.252	0.025
Lodgepole	0.191	0.016	0.199	0.017
Burned ponderosa	0.275	0.025	0.318	0.022
Wet meadow	0.202	0.040	0.199	0.030
	0.194†	0.026	0.199†	0.022
Dry meadow	0.435	0.031	0.470	0.039
	0.284‡	0.005	0.305‡	0.014
Ponderosa	0.331	0.021	0.323	0.208
	0.254†	0.021	0.283†	0.021

† Based on $n = 5$ plots (5000 m²).
‡ Based on $n = 3$ plots (3000 m²).

Species–area curve corrections

Species–area curves not corrected by the mean Jaccard's coefficient greatly underestimated species richness (Table 2). For example, the uncorrected, average species–area curve would estimate only 28 species in 4000 m² of lodgepole pine forest, although 88 species were observed in the four 1000-m² plots. Correcting the species–area curves, based only on the mean Jaccard's coefficient information from the 1 m², 10 m², and 100 m² species data, substantially improved the accuracy of the estimated number of species. Thus, fairly accurate estimates can be made of the number of species in an area 10 times larger than the sample area (e.g., when 520-m² data were used to predict the number of species in 4000 m²).

The accuracy of the predictions of species richness was improved further in three ways. First, additional information on species overlap from the 1000-m² plots (J_{1000}) greatly improved species richness estimates for the aspen, lodgepole, and burned ponderosa pine types, without adding additional field plots (Table 2). Second, adding one more field plot greatly improved species richness estimates in the ponderosa pine type, from a 13.8% difference to a 3.4% difference in observed vs. predicted values. Adding one more field plot in the wet meadow type slightly increased the accuracy of predicted species area richness from 85.2% to 88.5% (Table 2). Third, removing obvious outliers in the pairwise J values greatly increased the accuracy of predictions of species richness in the wet meadow type: removing one outlier in the 10 pairwise comparisons improved accuracy to 92.6%, whereas removing two outliers improved accuracy to 98.0% (Table 2). Thus, species–area curves in the six vegetation types ranged in accuracy from 99.3% (aspen) to 95.3% (dry meadow).

The accuracy of the species–area curve for the dry meadow type was influenced by spatial autocorrelation. Two of the four randomly selected vegetation plots in the dry meadow type were located within 100 m of each other, and thus had a within-type species overlap ($J = 0.648$) three times greater than most of the other J values. When one of the two neighboring plots was removed from the analysis, spatial autocorrelation effects were reduced and accuracy of the species richness estimate improved considerably (Table 2).

The corrected species–area curves varied by vege-

TABLE 2. Observed and estimated numbers of species, based on species–area curves (S–A curves) from 1-m², 10-m², and 100-m² subplot data on species richness for vegetation types in the Beaver Meadows area of Rocky Mountain National Park, Colorado. Estimates are presented with and without correction (corr.).

		Estimated number of species			
Community type	Observed no. spp.	S–A curve (no corr.)	S–A curve (J_{100} corr.)	S–A curve (J_{1000} corr.)	Sample area (m²)
Aspen	150	63	161	149	4000
Lodgepole	88	28	95	91	4000
Burned	59	24	66	58	1000
Wet meadow	122	44	103	104	4000
	148	51	134	131	5000
				(145)†	
Dry meadow	83	48	72	69	4000
	81	45	89	85	3000
Ponderosa	80	43	89	91	4000
	88	38	99	91	3000

† Two outliers of Jaccard's coefficient were removed ($n = 8$ values left).

TABLE 3. Species–area curves, corrected with Jaccard's coefficient for vegetation types in the Beaver Meadows area of Rocky Mountain National Park, where y = cumulative species, m = slope, J = Jaccard's coefficient, and b = constant. Coefficients of determination were based on the original uncorrected curves, using the average cumulative species in 1-m², 10-m², and 100-m² subplots, and 1000-m² plots.

Vegetation type	Equation $y = m/J(\log \text{area}) + b$	r^2
Dry meadow	$y = 5.70/0.305(\log \text{area}) + 31.20$	0.992
Wet meadow	$y = 6.16/0.199(\log \text{area}) + 30.56$	0.988
Aspen	$y = 9.58/0.252(\log \text{area}) + 33.20$	0.982
Ponderosa pine	$y = 5.76/0.283(\log \text{area}) + 17.36$	0.992
Burned ponderosa	$y = 5.95/0.318(\log \text{area}) + 7.32$	0.955
Lodgepole pine	$y = 7.22/0.199(\log \text{area}) + 10.48$	0.903

tation type (Table 3). The slopes of the species–area curves ranged from $m = 5.70$ in the dry meadow type to $m = 9.58$ in the aspen vegetation type. The constants for the equations were up to four times higher for the aspen, wet meadow, and dry meadow communities than for the pine types.

Species overlap among vegetation types

Species overlap varied greatly among vegetation types (Table 4). Species composition of the wet meadow vegetation type overlapped 21.8% with the aspen community type, but <14% with the other vegetation types. The cross-comparisons of the ponderosa pine, burned ponderosa pine, and lodgepole pine types had between 28% and 31% overlap. Although the wet meadow and dry meadow communities were close to each other on the landscape, their species composition overlapped only 16.3%.

Vegetation patterns resulting from different MMUs

Describing vegetation patterns with large MMUs may significantly underestimate plant community diversity, the number of polygons (e.g., habitat patches and landscape complexity), and total plant species richness (Fig. 4; Table 5). At the 0.02-ha scale, six vegetation types were recognized, including the aspen type that was scattered in clumps throughout the landscape. With the 2-ha MMU, five vegetation types were recognized for the study area. The aspen type was absent, and the size of burned ponderosa pine habitat was half of that recognized with the 0.02-ha MMU. The number of polygons delineated was three times greater for the 0.02-ha MMU map than for the 2-ha MMU map. With the 50-ha MMU, four vegetation types were recognized in the study area (Table 5); the species-rich aspen type and the burned ponderosa pine type were noticeably absent. The resulting vegetation map had only six polygons, yet the estimated plant species richness was 439 species, or 87.3% of the total estimated from the map with the finest resolution (0.02-ha MMU). With the 100-ha MMU, only three vegetation types were recognized in our study area: lodgepole pine, dry meadow, and ponderosa pine. The vegetation map contained only three polygons (Fig. 4), and 341 plant species were estimated from the species–area curves (corrected for overlap).

Contribution of vegetation types to total plant species richness

By incorporating the areal coverage estimates of the vegetation types into the species–area curves, we can estimate the total species richness for each vegetation type in the study area (Table 6). We would estimate, for example, that the 8.8 ha of aspen type would contain ≈221 plant species (95% CI = 205–237 plant species), whereas the 141.4 ha of lodgepole pine would contain ≈233 plant species (95% CI = 217–249 plant species). The ponderosa pine and dry meadow types would contain a low number of species relative to their areal extent on the landscape.

The wet meadow and aspen vegetation types contained the highest number of unique species, 76 and 50 species, respectively, observed in the plots. However, these unique species occurred in vegetation types that are not likely to be recognized with larger minimum mapping units. Considering their large combined area, the pine community types contained relatively few plant species (Table 6).

TABLE 4. Proportion of plant species shared between vegetation types in the Rocky Mountain National Park.

Vegetation type	Wet meadow	Aspen	Ponderosa	Burned ponderosa	Lodgepole pine
Dry meadow	0.163	0.200	0.367	0.211	0.226
Wet meadow		0.279	0.140	0.107	0.140
Aspen			0.259	0.194	0.273
Ponderosa				0.313	0.285
Burned					0.301

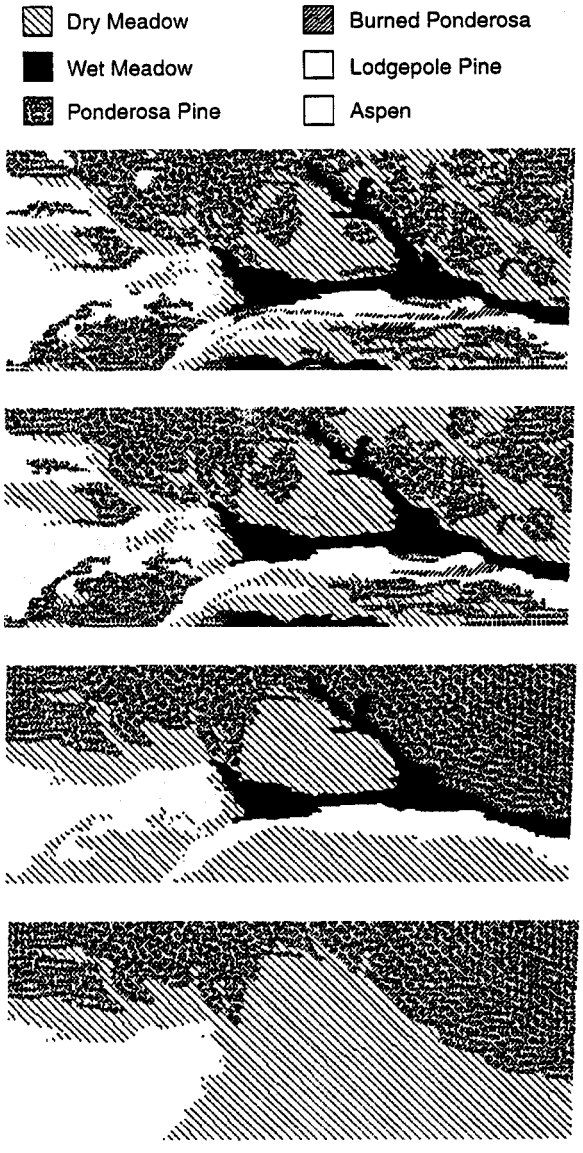

FIG. 4. Vegetation type maps with minimum mapping units of (top to bottom, respectively) 0.02 ha, 2 ha, 50 ha, and 100 ha.

To estimate the number of plant species that occur in the Beaver Meadows landscape, we estimated the total number of species found in each type, using species–area curves corrected with Jaccard's coefficient (J). We then sequentially composited the estimated lists from each vegetation type, correcting each composited list with the estimated species overlap (J). Thus, we estimated that 552 plant species (95% CI = 520–583 plant species) could be found in the 754-ha study area (Fig. 5), a reasonable number, considering that we found 330 plant species in 2.2 ha (within the vegetation plots).

DISCUSSION

The use of multiscale techniques

Multiscale techniques allowed us to quantify plant diversity patterns in the 754-ha study area in a few weeks of sampling. Because we corrected for heterogeneity within vegetation types, accurate species–area curves could be developed with only three to five replicate plots per type. In five of the six vegetation types we studied, our predictions were off by <4% of the observed values, with estimates for the dry meadow type off by <5% (Table 2). Because we can accurately estimate the number of species in an area 10 times larger than the area used to create the species–area curves, we are confident that we can accurately estimate the number of plant species found in much larger areas.

Species–area curves are influenced by sample size, variation in species richness at multiple scales, and species overlap. There are obvious trends toward decreasing the variance with only slight increases in sample size, because adding one plot adds numerous, paired Jaccard's coefficients. Four of the six vegetation types were described well by using four or fewer sample plots. Two vegetation types were adequately described with five plots. One plot takes a team of two people 2–3 h to complete. The multiscale vegetation plots worked equally well in large vegetation communities (e.g., lodgepole pine) and small habitats (e.g., aspen, burned areas). Changing the size of the plots from 20 × 50 m in most vegetation types to 10 × 25 m in the burned ponderosa pine type did not affect the behavior of the process: in either case, accurate assessments could be made of species richness in larger areas (Table 2), and species overlap within and between vegetation types (Tables 1 and 4).

We were extremely efficient at capturing a large proportion of the number of known plant species in Rocky Mountain National Park. Sampling occurred within an elevation range of 2500–3000 m and did not encompass subalpine, alpine tundra, and lower elevation riparian zones, which we plan to sample next summer. Still, we recorded 330 plant species (≈one-third the number of plants recorded in the Park) in the 2.2-ha area within the plots, and estimated 552 plant species (≈one-half the number of plants recorded in the Park) in the 754-ha sampling area. Also, the cumulative estimated number of plant species leveled off considerably as the cumulative area increased, as one would expect (Fig. 5). This suggests that: (1) multiple-scale sampling techniques may be very efficient in conducting landscape-scale plant surveys in areas with poor existing data, i.e., most natural areas (Stohlgren et al. 1995*b*); and (2) plant species distribution patterns may be highly redundant within larger landscapes in the same ecoregion.

Capturing one-third the number of plant species in the 1074-km^2 Rocky Mountain National Park in just 25 plots (0.025–1.0 ha) suggests that existing vegetation maps in many national parks could be improved substantially. Maps that usually contain information only on overstory types could be improved with a minimal amount of field work by conducting multiscale

TABLE 5. Vegetation types recognized, area of each type (ha; main table entries for each vegetation type), number of polygons recorded (in parentheses), and estimated total plant species richness for different minimum mapping units.

	Minimum mapping unit (ha)			
	100	50	2	0.02
Vegetation type				
Lodgepole	132.0 (1)	137.4 (2)	147.5 (9)	141.4 (16)
Ponderosa	281.0 (1)	281.0 (1)	266.0 (20)	269.9 (48)
Dry meadow	340.8 (1)	279.4 (2)	270.1 (7)	260.8 (31)
Wet meadow		56.0 (1)	65.4 (2)	63.1 (3)
Burned ponderosa			4.7 (1)	9.8 (7)
Aspen				8.8 (12)
Total area (ha)	753.8	753.8	753.8	753.8
Total no. polygons	(3)	(6)	(39)	(117)
Estimated total no. plant species	341	439	473	522

plant surveys to quantify understory species richness, cover and distribution of non-indigenous plants, and locations of habitats with high-diversity or unique species assemblages. The species richness patterns that we found are being related to environmental variables (e.g., slope, aspect, and elevation) to develop a predictive plant diversity model (Buckley et al. 1993) to be validated with additional field work next year. Because plots are precisely located with a global positioning system and the data are collected within a GIS framework, they provide resource managers with a means to monitor long-term changes in plant diversity and weedy plant invasions, and to evaluate the effects of various land use practices on plant diversity. They also provide an independent data set to assess the accuracy of present and future vegetation maps (Kalkhan et al. 1995).

These multiscale sampling techniques could be used with high success in any area because they require a minimum amount of fieldwork. The efficiency is the result of: (1) recognizing potentially important vegetation types before stratification (small aspen stands and wetlands, in our case); (2) unbiased selection of plot locations within vegetation types; and (3) the multiscale sampling methods and corrections of species–area curves based on heterogeneity within vegetation types. The techniques are adaptable to a wide range of vegetation types, simply by adjusting the size of the modified-Whittaker plot (Stohlgren et al. 1995*a*). For example, we used 0.025-ha plots in some closed-canopy forest types and in alpine tundra, but larger plots may be necessary in eastern United States deciduous forests and in tropical rain forests. The most important requirements of the technique are to stratify common and rare vegetation types, to select unbiased sampling sites, to include four scales of sampling (e.g., the 1-m^2, 10-m^2, and 100-m^2 subplots from each 1000-m^2 plot for our area), and to select an appropriate minimum mapping unit.

Effects of minimum mapping unit size on evaluating patterns of plant species diversity

The size of the MMU greatly influences our potential understanding of plant diversity patterns in three ways.

TABLE 6. Total numbers of plant species and unique plant species observed (obs.; in plots) or estimated (est.; 0.02-ha MMU, Table 5) in the study area, and the estimated number of observations of new plant species/ha of habitat in the 754-ha study area (as an index of the relative contribution of vegetation types to the diversity of plants in the study area).

Vegetation type	No. spp. obs.	No. unique spp. obs.	No. spp. est.	No. spp./ ha est.
Dry meadow	81	31	116	0.44
Wet meadow	148	76	210	3.33
Aspen	150	50	221	25.17
Ponderosa	88	12	148	0.55
Burned ponderosa	59	10	101	10.25
Lodgepole pine	88	18	233	1.65
Totals (duplicates removed)	330	197	552	

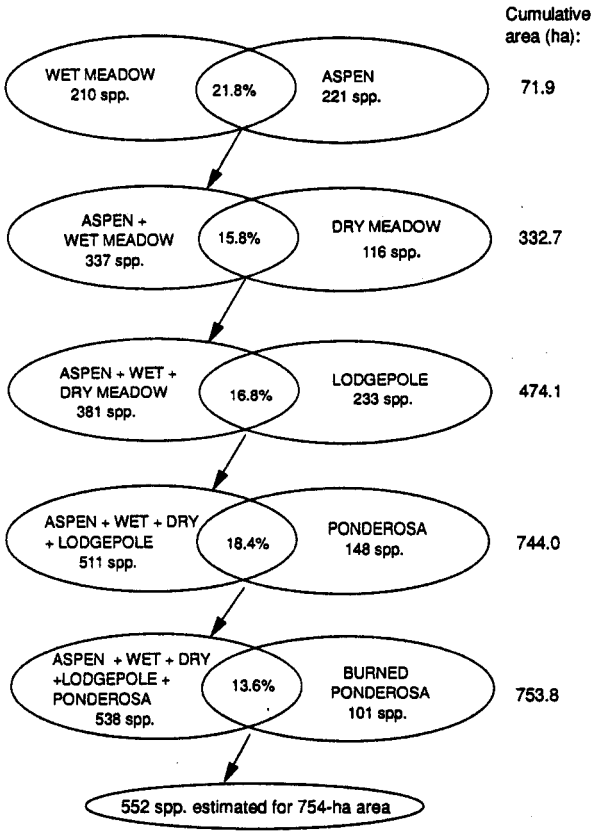

FIG. 5. Calculation of total plant species richness in the study area.

First, if the MMU is too large, some large-area vegetation types appear larger and more contiguous, some medium-area vegetation types appear reduced or increased in landscape cover, and some small-area vegetation types are entirely undetected (Fig. 4, Table 5). We expected that a vegetation map created with a 100-ha MMU (typically used in GAP Analysis; (Scott et al. 1993) would report only a few cover types in our study area. However, even with the 2-ha MMU (used in many states and National Park Service units), the species-rich aspen type would not be recognized. The 100-ha MMU Gap Analysis map currently in production for Colorado recognizes only two vegetation types in our study area (W. Reiners, University of Wyoming, *personal communication,* October 1995). That map, if used without ancillary data, may create the second type of gap in protection discussed in this paper: the gap created when important habitats, within or outside protected areas, are missed because they occur in patches too small to be recognized using a coarse mapping resolution.

The 2-ha MMU recovered 86% of the plant species, but failed to detect the aspen vegetation type (Fig. 4) and associated unique plant species (Table 6). The 2-ha MMU produced better information on species diversity patterns than the 50-ha or 100-ha MMU, but could have extreme repercussions in estimating wildlife diversity based on habitat availability. Peet (1981) showed that aspen stands were high in plant diversity, and we have demonstrated that the aspen stands also have steeper species–area curves, higher numbers of unique species, and little species overlap with other communities (except with the wet meadow type that also is rare on the landscape).

Second, increasing the MMU size in our study sharply decreased the number of polygons recognized (Table 5). If these polygons represent patches of important wildlife habitat, then our assumptions about habitat availability and connectivity may be influenced heavily by the resolution of vegetation maps. Too large a MMU may suggest the presence of large, contiguous habitat that does not really exist. Alternatively, important thin corridors or small patches of habitat (i.e., riparian zones, stands of aspen) may not be recognized on the vegetation map where they do exist in nature. For small mammals, amphibians, and patch-specific plants and invertebrates, these small sanctuaries could be the most important features for persistence, providing for the survival of populations and metapopulations throughout the landscape (Opdam et al. 1993).

The third major effect of large MMU size is simply that finished, brightly colored maps and GIS themes may lead to complacency: land managers may assume that additional research, inventory, and monitoring are not a priority. Vegetation maps of finer resolution can aid in the detection and management of rare species by identifying distinctive ecosystems. The aspen, wet meadow, and burned ponderosa vegetation types covered very small portions of the landscape, but contained a high proportion of the unique plant species. Thus, these types fell into the underdetected gap when the MMU was too large (for example, 2 ha was too large for the aspen type). In the study plots, we found 50 species that only occurred in the aspen type, 76 species that only occurred in the wet meadow, and 10 species that only occurred in the burned ponderosa type. Several rare species occurred in the wet meadow: lady's tresses orchid (*Spiranthes romanzoffiana*), wood lily (*Lilium philadelphicum*), and white bog-orchid (*Limnorchis dilatata* ssp. *albiflora*). Although these species are not on any Federal lists, they may be considered locally rare because their habitats are small and patchily distributed. Recognition of these small habitat types is crucial for calculating accurate estimates of biodiversity and suitable wildlife habitat.

Application and design considerations

Colwell and Coddington (1994) state that "the quantitative integration of richness and complementarity (i.e., biotic distinctness) presents an important but poorly studied challenge" in landscape ecology. Our methods address this challenge by correcting species–area relationships with Jaccard's coefficient. The complement of Jaccard's coefficient is biotic distinctness. We evaluate the effects of minimum mapping unit size

by: (1) initially stratifying homogeneous, heterogeneous, and rare habitat types; and (2) evaluating within-type and between-type heterogeneity generated by environmental gradients and other factors. We acknowledge that more research is needed to understand and refine species–area relationships in other areas.

Our approach can easily be extrapolated to larger landscapes and over broader environmental gradients. As additional multiscale plots are established within a vegetation type, the average pairwise Jaccard's coefficient is recalculated to evaluate within-type heterogeneity and new species–area curves are developed. Additional vegetation plots are established when increased variance is encountered in Jaccard's coefficient or in the slopes and intercept of the species–area curves. As new vegetation types are encountered, heterogeneity between vegetation types is recalculated.

We are currently evaluating the effects of spatial autocorrelation in our study design. We are finding that spatial autocorrelation is a dual-edged sword. Vegetation plots established too close together inflate the Jaccard's coefficient and, thus, the slope of the species–area relationship. However, spatial autocorrelation is an important component of plant species distributions, especially the invasion of non-native species. We are currently conducting an analysis of spatial autocorrelation and cross-correlation (e.g., environmental variables of slope, aspect, and elevation) for the study area.

Our study suggests that gaps in our current understanding of plant diversity patterns may be greatest at the landscape scale, and that more vegetation surveys linking plot data to regions are needed (Franklin 1993). Multiscale data on vegetation patterns collected from replicate study areas might provide a means to predict plant diversity patterns from coarse-resolution maps. Studies such as these could provide the critical linkage between statewide GAP Analysis programs and intensive studies within a landscape (Short and Hestbeck 1995). Rare vegetation types, such as aspen, wet meadows, and riparian areas, may still be underestimated with the 0.02-ha MMU, and their contribution to total biological diversity is probably greater than our estimates of plant diversity indicate. As our management strategies move away from a species-by-species approach to biological conservation, resource managers require better information on unique, locally rare habitats that are only apparent when small minimum mapping units are used. We suggest that at least some portions of vegetation maps created at a coarser level of resolution be validated at a higher level of resolution. Additional sampling and conservation efforts should be directed to these distinctive ecosystems.

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