Biodiversity and Conservation **12:** 255–278, 2003.

A nested-intensity design for surveying plant diversity

DAVID T. BARNETT[1,*] and THOMAS J. STOHLGREN[2]
[1]*Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499, USA;* [2]*Midcontinent Ecological Science Center, United States Geological Survey, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499, USA;* [*]*Author for correspondence (e-mail: barnett@nrel.colostate.edu)*

Received 12 June 2001; accepted in revised form 4 February 2002

Key words: Inventory, Nested-intensity designs, Plant species richness, Sample plot size

Abstract. Managers of natural landscapes need cost-efficient, accurate, and precise systems to inventory plant diversity. We investigated a nested-intensity sampling design to assess local and landscape-scale heterogeneity of plant species richness in aspen stands in southern Colorado, USA. The nested-intensity design used three vegetation sampling techniques: the Modified-Whittaker, a 1000-m^2 multiple-scale plot (n = 8); a 100-m^2 multiple-scale Intensive plot (n = 15); and a 100-m^2 single-scale Extensive plot (n = 28). The large Modified-Whittaker plot (1000 m^2) recorded greater species richness per plot than the other two sampling techniques ($P < 0.001$), estimated cover of a greater number of species in 1-m^2 subplots ($P < 0.018$), and captured 32 species missed by the smaller, more numerous 100-m^2 plots of the other designs. The Intensive plots extended the environmental gradient sampled, capturing 17 species missed by the other techniques, and improved species–area calculations. The greater number of Extensive plots further expanded the gradient sampled, and captured 18 additional species. The multi-scale Modified-Whittaker and Intensive designs allowed quantification of the slopes of species–area curves in the single-scale Extensive plots. Multiple linear regressions were able to predict the slope of species–area curves (adj R^2 = 0.64, $P < 0.001$) at each Extensive plot, allowing comparison of species richness at each sample location. Comparison of species–accumulation curves generated with each technique suggested that small, single-scale plot techniques might be very misleading because they underestimate species richness by missing locally rare species at every site. A combination of large and small multi-scale and single-scale plots greatly improves our understanding of native and exotic plant diversity patterns.

Introduction

Land-use change, exotic species invasion, and the lack of basic information threaten natural landscapes. Successful stewardship of such landscapes hinges on a manager understanding both the processes that threaten the landscape, and the resulting resource pattern and condition. Understanding resource condition – inventory (Stohlgren 1994; Peterson et al. 1995; Nusser and Goebel 1997), and change through subsequent measurement – monitoring (Mulder et al. 1999) establishes an investigation and feedback loop capable of directing management. The variability inherent in all natural landscapes challenges inventory accuracy, and mandates that investigations consider local and landscape scales. However, large, multi-scale and spatially extensive investigations require an abundance of funding and time unavailable to most managers. This paper explores a method that addresses the challenges associated with making an accurate and cost-effective inventory accessible to land managers.

Heterogeneous plant species distributions make inventories difficult. Ecologists traditionally ignored this variability with assumptions that simplified complexity (Levin 1992). For example, Parker (1951) and Daubenmire (1959) transects use linear, small-scale methods to assess vegetation in sites presumed to be representative of a homogeneous landscape. Changing ecological paradigms led plant ecologists to focus on landscape heterogeneity (Shmida 1984; Stohlgren et al. 1995, 1997c, 2000; Kotliar 1996). Robert Whittaker (Shmida 1984) and Stohlgren et al. (1995) developed multi-scale vegetation sampling methods that greatly increased the area sampled (about 500 times more area than the 20, 50×20 cm^2 Daubenmire quadrats) and reduced spatial autocorrelation inherent in many transect and quadrat methods (Stohlgren et al. 1998a). These large, multi-scale plot designs detected 45–79% more species than a typical Daubenmire transect, and 66% more species than the Parker transect (Stohlgren et al. 1998a), providing a more accurate description of local plant species richness.

While local characterizations are important, managers also need systems of inventory and monitoring that assess large areas. Land managers need to understand the appropriate sample size and method, and understand how both might change as data are collected and new questions are considered. Furthermore, because ecological investigations can only afford to sample a small portion of a landscape, extrapolation to unsampled regions must be done carefully (Krebs 1989; Turner 1989; Stohlgren et al. 1997c). Increasing sample size, distribution, and variety of scales sampled accounts for a higher degree of the spatial heterogeneity across a landscape (Stohlgren et al. 2000). Methods such as ‘double sampling’, that increase sample size and efficiency are not new to ecology. Range ecologists have long used ocular estimates of biomass and sub-samples of clipping and weighing actual biomass to improve biomass estimates of large grazing allotments (Bonham 1989). Similarly, Kalkhan et al. (1998) used double sampling to efficiently estimate the accuracy of vegetation type characterizations from a Landsat Thematic Mapper (TM) classification map. A few ground plots were used to correct for misclassification errors between Landsat TM data and aerial photographs. The variety of sampling intensity applied in double sampling provides managers with an effective means for quantifying landscape-scale variation, as sample size can be increased at a reduced cost.

Limited budgets and large landscapes make accurate and useful inventories difficult to design and present managers interested in landscape condition and trend with several trade-offs (Stohlgren 1994; Nusser and Goebel 1997):

1. Large plots may provide a good picture of local vegetation conditions, but the use of these thorough plots at several locations may limit the number of plots that can be placed on the landscape. Quality information at localized points may sacrifice understanding of landscape pattern.
2. More small plots may increase the quality of broad-scale pattern description, but the quantity of these plots may limit the information collected at each site. Spatial extent is increased at the expense of detailed understanding at local scales.

3. Simple, single-scale sampling designs may provide accurate and precise data, but may not be cost effective for managers. Intricate methods for inventory are often not used by managers due to their complexity.

In this paper, we present a 'nested-intensity design' that addresses the challenges of these trade-offs. We used three plot designs to measure native and exotic plant species richness and cover and species–area curves to evaluate the effectiveness of this design at describing local and landscape patterns of plant species richness. We also measured aspen (*Populus tremuloides*) stand structure to evaluate the applicability of this design to other inventory measurements. The three designs included a large, multi-scale plot; a smaller multi-scale plot; and a single-scale plot. To assess effectiveness of the nested-intensity design we asked the following questions: (1) What are the advantages and disadvantages associated with the three vegetation sampling plot designs? (2) What are the benefits of using a suite of plot designs in a nested-intensity framework? (3) How do different vegetation sampling plot designs influence species–accumulation curves? (4) How can nested-intensity designs facilitate land management?

Methods

Site description

The sampling took place in aspen vegetation on a ranch on the western slope of the spine-like Sangre de Cristo mountain range in south-central Colorado, USA. The Culebra group, the southern subsection of the Sangre de Cristo, stretches north for 50 km from the New Mexico border, bisecting the shortgrass steppe of Colorado to the east, and the San Luis Valley to the west. The elevation of this mountainous ranch ranges from approximately 2600 to 4267 m at the top of Culebra Peak. The vegetation reflects this varied topography. A relatively thin band of grasslands and sagebrush (several species of *Atremisia*) lines the lower reaches of the western property line. Forested vegetation types include ponderosa pine (*Pinus ponderosa*), douglas fir (*Pseudotsuga menziesii*), Englemann spruce (*Picea engelmannii*), subalpine fir (*Aibes lasiocarpa*), and aspen. Tundra and an abundance of alpine rock dominate higher elevations.

Sampling was limited to aspen as the vegetation type covers approximately 10 000 ha of the 30 000 ha ranch, and because aspen supports floral (Stohlgren et al. 1997a), butterfly (Simonson et al. 2001), and bird (DeByle 1985) diversity otherwise rare in the landscape. The success of aspen regeneration is of concern in similar regions across the Rocky Mountains (Romme et al. 1995).

Plot designs and vegetation sampling

The boundary of the ranch at the time of sampling created the extent of the study area. The southern portion of the ranch belonged to a different owner, so we excluded this portion of the ranch from the study area extent. We stratified aspen vegetation using high-resolution aerial photographs (1:24 000) from 1997. Random points were located within the aspen and assigned to one of three vegetation-sampling methods. The nested-intensity design included three vegetation-sampling methods. To describe the aspen landscape, we collected detailed data at a few points to understand local patterns, and less detailed data at more points to quantify landscape-scale variation. As the design is intended to describe patterns of diversity, we evaluated the efficiency and effectiveness of the various components of the design in a field environment. Complex landscapes with multiple environments are difficult, impractical to recreate and may not represent realistic costs or design comparisons.

We randomly located eight Modified-Whittaker plots (Stohlgren et al. 1995, 1997b, c, 1998a) on the landscape. The Modified-Whittaker plot contained 10 1-m^2 non-overlapping subplots, two 10-m^2 non-overlapping subplots, and one 100-m^2 subplot, all nested within the 1000-m^2 (20×50 m^2) plot (Figure 1a). In each of the 1-m^2 subplots, we identified all vascular plant species and estimated the average height and cover to the nearest percent for each species. We also recorded the species presence in the 10- and 100-m^2 subplots, and in the 1000-m^2 plot.

Based on the design of the Modified-Whittaker plot, we developed the 'Intensive' plot (Figure 1b) for the purposes of this study. We placed 10 Intensive plots across the landscape, intermixed with the Modified-Whittaker plots. The Intensive plot contained four 1-m^2 subplots and one 10-m^2 subplot, both nested within a 100-m^2 plot. In each of the 1-m^2 subplots, we identified all vascular plant species and estimated the cover to the nearest percent for each species. In the 10-m^2 subplot and 100-m^2 plot, we recorded the presence of all vascular plant species.

We established 30 'Extensive' plots, dispersed among other sample design locations. Designed for this study, the Extensive plot required the least effort and returned the least amount of information. Species presence was recorded in the 100-m^2 plot, but no evaluation of subplots or species cover occurred in this plot (Figure 1c).

We referenced the location of each plot with the global positioning system and collected ancillary data on aspect, elevation, and slope. We recorded the time required to sample each plot, and the total travel time. All plant specimens were identified to species following the National Plants Database Nomenclature (USDA, NRCS 2001). Plants that could not be identified (due to grazing or missing flower parts) were given a unique identification code and counted as a single species to avoid inflating species richness estimates. Species that could be identified only to genus were recorded in the database, and all samples of one genus were considered to be of the same identity.

We evaluated aspen stand structure in one-half of every 100-m^2 plot. We divided the 100-m^2 plot into two 50-m^2 plots, and evaluated the aspen stand structure in one of these randomly selected 50-m^2 plots. In the Modified-Whittaker and Intensive plots, the diameter at breast height (dbh) in cm was recorded for every tree. Less information was collected at Extensive plot locations. For all stems over 2 m tall, we recorded whether the tree was alive or dead, was $>$ or $<$10 cm dbh, and the average

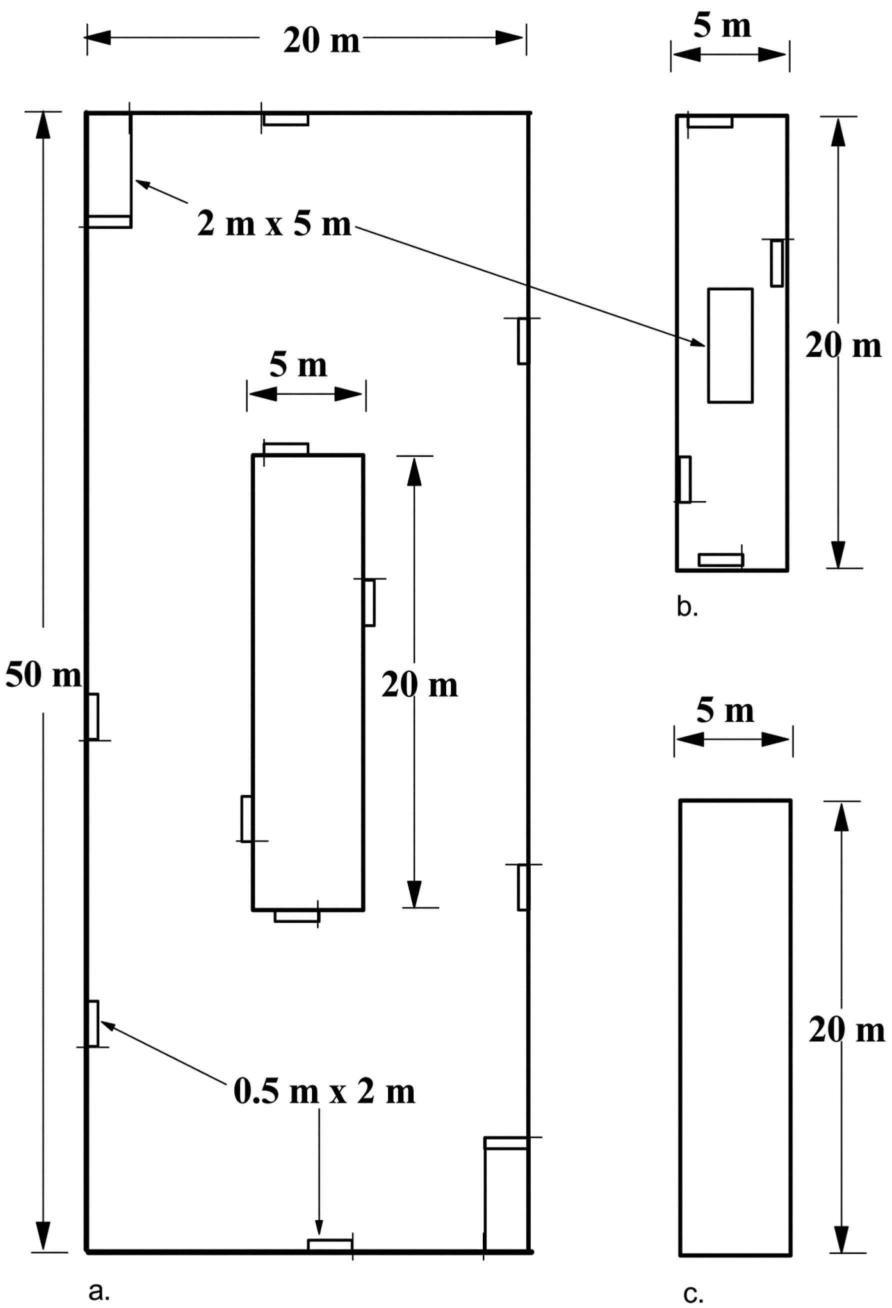

Figure 1. The layout of the (a) Modified-Whittaker, (b) Intensive plot, and (c) Extensive plot as used in the nested-intensity inventory effort.

% browse. For all stems <2 m tall, the number of stems and whether the tree was alive or dead was recorded.

We considered stems >2 m tall and <10 cm dbh representative of recent successful canopy recruitment. Once a stem grows over 2 m, the top of the stem is usually tall enough to be above the browsing reach of most elk. Ripple and Larsen (2000) determined that stems of 10 cm dbh on the northern range of Yellowstone National Park were between 10 and 30 years old. Other investigations have used similar diameters as evidence of the presence of younger stem regeneration (Krebill 1972; Baker et al. 1997). The exact age to size ratio is not as important as the presence of pole-like stems indicative of a younger cohort or stem in a stand.

Statistical analyses

We compared plant species richness, total species detected, and total unique species captured between the three vegetation sampling techniques. A species detected or captured only by one particular sample design defined a unique species. Moran's *I* was used to check the species richness of the 100 m^2 for spatial autocorrelation using spatial applications (Reich and David 1998) in the S-Plus statistical package (MathSoft Inc. 1999). All other analyses, except where noted, were carried out using SYSTAT (SPSS Inc. 2000).

To increase efficiency, we frequently sampled with more than one design in a single day. To calculate the total time required to complete the entire sampling of each design, including travel time, we subtracted the time to sample each plot in a single day from the length of the day to yield time required for travel. Travel time was divided equally among the number of plots sampled that day. Travel time and sample time for each design were totalled within a given day and across the number of total sampling days. The average time required to sample with each design was also calculated and compared using analysis of variance.

We compared the average species richness per plot, and the average species richness in the 100-m^2 subplot (Modified-Whittaker plot design) or plot (Intensive and Extensive plot designs), from each plot type using analysis of covariance. We also plotted the number of species in the 100-m^2 plots against each other to examine potential bias of the techniques.

We compared Modified-Whittaker and Intensive plot plant richness totals at the 1- and 10-m^2 subplots with *t*-tests. These totals differ from previously described subplot means of the species richness. The total numbers of species detected within each subplot size at each plot were accumulated for this purpose. Comparison of plot species totals in 100-m^2 plots between the three techniques were not warranted, as no replicates of this plot size were recorded and comparisons would be identical to plant species richness at this scale.

We calculated the species–accumulation curves for each design. A species–accumulation curve describes the rate at which a particular sampling technique adds new species to the species list for that technique as more plots are placed on the landscape. We also created species–accumulation curves that described the contribution of each sampling technique to the total species list generated by all three techniques combined. For example, one iteration initiated the curve with the species detected using the Modified-Whittaker plots. The second section of the curve was defined by the new species accumulated with the addition of the Intensive plots on the landscape, and the third portion of the curve was dictated by the addition of species detected by the Extensive plots and not detected previously by the other techniques. Using this method, we built total species–accumulation curves in several combinations: the Intensive plots, Extensive plots, Modified-Whittaker plots; and the Extensive plots, Modified-Whittaker plots, Intensive plots. All curves were created using Estimates (Colwell 1997), a program that computes randomized species–accumulation curves, thus removing the effect of the order in which each plot was placed on the landscape.

Species–area curves

A species–area curve defines the rate at which species numbers increase with increases in area (Rosenzweig 1995). Species–area curves could only be calculated for the Modified-Whittaker and Intensive sampling methods, as the Extensive design contained no nested subplots. To generate species–area curves at each appropriate sampling location, we calculated the mean number of species in the 1- and 10-m^2 subplots, and the total number of species in the 100-m^2 subplot and 1000-m^2 plot for each Modified-Whittaker plot. Similarly, we calculated the mean number of species in the 1-m^2 subplots, and the total number of species in the 10-m^2 subplot and 100-m^2 plot of the Intensive plots.

Two commonly used models for building species–area curves were selected from the literature as candidate models to fit species–area curves; the exponential model and the power model (Rosenzweig 1995; Flather 1996; Leitner and Rosenzweig 1997; Harte et al. 1999). The power model has an equation of the form:

$$S = cA^z \tag{1}$$

where S represented the number of species, A the area, and c and z were constants. For the purposes of this study, and many others, the power function was manipulated in log–log form:

$$\log(S) = z\log(A) + \log(c) \tag{2}$$

The exponential model, applied in semi-log form, has an equation of the form:

$$\log(S) = A + z\log(c) \tag{3}$$

Both models describe species–area functions in linear form. We used a method of confrontational modeling (Burnham and Anderson 1998) to select the model that most accurately described the plant species richness data collected by the Modified-Whittaker and Intensive designs. Model parameters were estimated by minimizing the sum of squared errors. The maximum log-likelihood for each observation was calculated and used to calculate small sample Akaike Information Criteria (AICc),

Δr, and the Akaike Weights for each model (Burnham and Anderson 1998). The model associated with the lower small sample AIC indicates the model that most accurately describes the data. Δr is an indicator of models that have sufficient support given the data and should be considered; models with $\Delta r \leq 2$ should be considered. Akaike Weight accounts for uncertainty in the order of model ranking given error in the data, and frames the model selection as a probability (Burnham and Anderson 1998).

Average species–area curves were then fitted for the Modified-Whittaker and Intensive sampling techniques based on the model that best described the data as noted above. The slopes of these lines were compared using the general linear model in the SAS statistical package (SAS Institute 1998). Using the model that best described the curves, we derived species–area curves and the slope of the curves for each Modified-Whittaker and Intensive plot location based on the subplot and plot data.

Based on data from the Modified-Whittaker and Intensive designs, we created a multiple linear regression to describe the slope of species–area curves at the Modified-Whittaker and Intensive plots in an attempt to estimate species–area curve slopes at locations sampled with the single-scale Extensive plots. We assessed the validity of the model by iteratively removing one Modified-Whittaker plot from the model at a time, rebuilding the model, and then comparing the observed and predicted slopes for the removed plot (repeated five times). To estimate the slope of the species–area curve at the single-scale Extensive plots, we plugged data collected at the Extensive plots into the model that described the slope of the Modified-Whittaker and Intensive plot species–area curves.

To fulfill the requirements of the model that described the slope of species–area curves at the Modified-Whittaker and Intensive plots, it was necessary to predict the dbh of live aspen stems in the extensive plots based on the number of live stems both >2 m and <2 m. Because dbh of live aspen stems was not collected at the Extensive plots, we developed another model with the Modified-Whittaker and Intensive plot data that predicted live dbh (adj $R^2 = 0.89$, $P < 0.001$) using the number of live stems $<$ and >2 m. We collected the number of stems $<$ and $>$ 2 m in the Extensive plots and were able to estimate live dbh at the Extensive plot with the dbh model created using the Modified Whittaker and Intensive aspen data. Lastly, multiple linear regression was used to generate a model that described the number of species in 100-m^2 plots in both the Modified-Whittaker and Intensive plot designs.

Results

Each Modified-Whittaker plot took longer to sample but captured more species than the smaller, simpler sampling techniques. However, sampling all of the plots of each technique required a similar amount of time when travel was included, and each technique accumulated a similar number of total species. Despite these equalities, the Modified-Whittaker still collected more unique species than the other two

Table 1. The total number of plots sampled and the time required to sample each plot of the nested-intensity design as sampled in the Sangre de Cristo mountains of Colorado.

	Modified-Whittaker plot (1000 m^2)	Intensive plot (100 m^2)	Extensive plot (100 m^2)
Number of plots	8	15	28
Mean h/plot at a site	6.7 $(0.86)_a$	2.8 $(0.9)_b$	0.47 $(0.1)_c$
Total sampling time (h)	53.6	42	13.1
Total travel time (h)	27.5	41.9	57.7
Total sampling and travel time (h)	81.8	83.9	70.8

The standard error of the mean appears in parentheses. The subscripts (a–c) signify significant difference between labeled values, $\alpha = 0.05$.

techniques. Regression models based on combinations of these techniques proved to be useful in predicting data not collected at the simpler Extensive plot. We present results in three sections, the plot type comparisons, comparison of species–area curves, and predictive models. A Moran's I value of -0.062 suggested that species richness in the 100-m^2 plot or subplot was spatially independent, so traditional statistical procedures were applied in the analyses.

How the various plot designs captured plant diversity

Modified-Whittaker plots required greater sampling time than the Intensive plots, which took longer to sample than an average Extensive plot ($P < 0.001$; Table 1). However, sampling and traveling to all plots of each design required a similar amount of time (Table 1). A greater number of Extensive plots and the travel time associated with sampling each plot (Table 1) greatly increased the time required to sample the methods with larger sample sizes.

The Modified-Whittaker plots (1000 m^2) detected more species per plot than both the Intensive (100 m^2) and Extensive (100 m^2) plot types ($P < 0.001$; Table 2). Because the various plots were not iteratively sampled at the same location, site variation could have affected these results. However, comparison of the 100-m^2 plot size yielded no statistical difference ($P = 0.19$) between the three sample techniques (Table 2). Furthermore, plots of species richness in the 100-m^2 plots or subplots suggested there was no systematic bias associated with the designs.

Unlike measures of plant species richness in the 100-m^2 plots, total species per subplot proved significantly greater at both the 1-m^2 ($P = 0.018$) and 10-m^2 ($P = 0.015$) subplots of the Modified-Whittaker as compared to the Intensive plots (Table 2). At both subplot scales, the greater distribution of subplots and the greater abundance of subplots in the Modified-Whittaker plot ($n = 10$) as compared to the Intensive plot ($n = 4$) resulted in a larger and more dispersed total area sampled. This difference quantifies the effect of having 10 subplots of 1 m^2 in the Modified-Whittaker design.

Despite different sample sizes and total sample area, the three test designs captured similar numbers of cumulative species (Table 2). However, the Modified-

Table 2. Comparisons of the three different vegetation sampling techniques used as components of the nested-intensity inventory in the Sangre de Cristo mountains of Colorado.

	Modified-Whittaker plot (1000 m^2)	Intensive plot (100 m^2)	Extensive plot (100 m^2)
Maximum plot area (m^2)	1000	100	100
Total area sampled (m^2)	8000	1500	2800
Mean species richness	56 $(8.8)_a$	30 $(2.7)_b$	25 $(1.4)_b$
Mean 100-m^2 species richness	29 (1.9)	30 (2.7)	25 (1.4)
Cumulative species richness	122	112	122
Cumulative exotic species richness	7	6	7
Number of unique species	32	18	14
Number of unique exotic species	2	1	1
Mean 10-m^2 species totals	26 $(5.3)_a$ $n = 2$/plot	18 $(8.2)_b$ $n = 1$/plot	
Mean 1-m^2 species totals	25.8 $(5.7)_a$ $n = 10$/plot	18.8 $(7.1)_b$ $n = 4$/plot	

The standard error of the mean appears in parentheses. Different subscripts (a, b) signify significant difference between labeled values, $\alpha = 0.05$.

Whittaker plots detected more unique species than the other two designs (Table 2). Of the species detected by the Modified-Whittaker plot, 25.8% were unique species as compared to 14.7 and 14.4% captured by the Intensive and Extensive plots, respectively.

The species–accumulation curve of the Modified-Whittaker plot increased at a faster rate than the curves of the smaller designs (Figure 2). The total number of new species increased with the addition of new plots (Figure 2). Early plots contributed more new species to the species lists than later plots that detect many species previously measured by other plots. We also determined the contribution of each design to the total species list accrued from the suite of the designs. When we fit this accumulation by alternating the order of each design's contribution to the species list, we found that: (1) the shape of the curve was significantly affected by the order of the inclusion; and (2) adding large-area plots, at any time, caused significant jumps in species–accumulation curves (Figure 3).

Species–area curves and predictive models

Model selection criteria metrics (Burnham and Anderson 1998) suggested that the power function provided the best description of the plant species richness data collected (Akaike Weight = 0.99; Table 3). A general linear model used to compare the average slopes of the species–area curves generated by the Modified-Whittaker and Intensive sampling techniques indicated that the slopes of these two lines were not significantly different ($P = 0.98$), and therefore the multi-scale richness data from the Modified-Whittaker and Intensive design could be pooled in an effort to predict the slope of unmeasured species–area curves at the Extensive plots.

Ancillary data, species richness in 100-m^2 plots or subplots, and diameter of live aspen stems allowed estimation of the slopes of the species–area curves of the Modified-Whittaker and Intensive sample designs (adj $R^2 = 0.64$, $F = P < 0.001$),

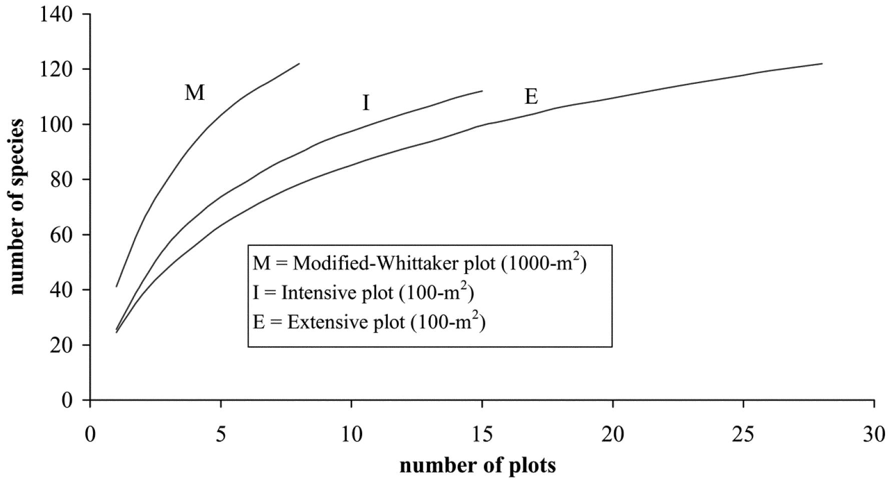

Figure 2. The species accumulation curves for each sample design.

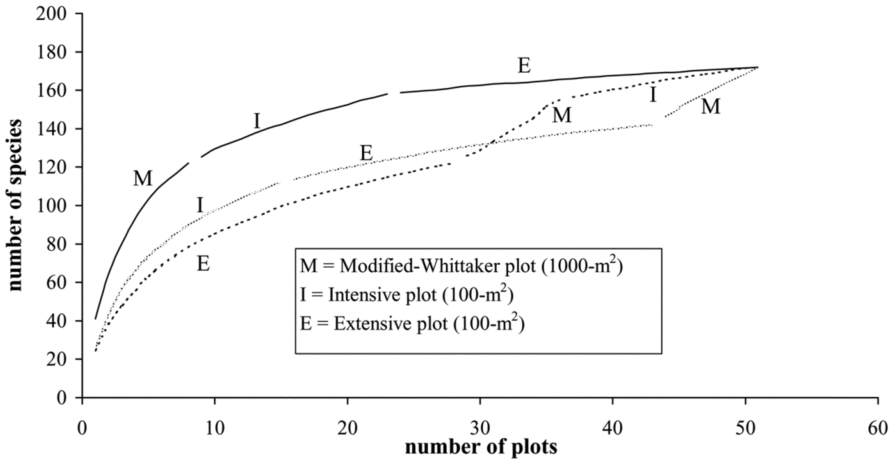

Figure 3. Species accumulation curves for the total number of species detected. The three curves demonstrate the contribution of each technique to the total number of species detected had all of the plots of each technique been sampled in the variety of orders displayed.

Table 3. Confrontation model selection metrics for selection of a species–area curve to fit multiple-scale data from Modified-Whittaker and Intensive design vegetation sampling techniques.

Model	Small sample AIC	Δr	Akaike weight
Exponential	555.9	295.6	0.00007
Power	536.8	276.5	0.999

and proved to be 96% accurate when validated. The following equation describes the relationship between the slope of the species–area curve and other variables collected (standard errors for coefficients appear below the coefficient):

$$\underset{(1705.7)}{\text{Slope}=8579.7}-\underset{(0.004)}{0.017}\times \text{UTM}x-\underset{(0.1)}{0.4}\times\text{aspect}-\underset{(0.76)}{1.8}\times\text{species in } 100\text{ m}^2+\underset{(14.08)}{37.3}\times\text{aspen (dbh)}$$

$$n=23 \qquad S_{xy}=28.3 \qquad R^2=0.70 \tag{4}$$

The model in Equation 4 was built based on the data from the Modified-Whittaker and Intensive plots, with the intention of predicting the slope of the species–area curve at each Extensive plot. However, because we did not measure the diameter of stems in the Extensive plot, we used another multiple linear regression model (adj $R^2 = 0.88$, $P < 0.001$) to predict the live dbh of aspen using the number of stems with dbh >10 cm and the number of stems with dbh <10 cm; the standard error of the coefficients appears below each coefficient:

$$\underset{(10.169)}{\text{Dbh}=13.041}+\underset{(1.345)}{17.156}\times\#\text{stems}>10\text{ cm dbh}+\underset{(0.825)}{3.149}\times\#\text{stems}<10\text{ cm dbh}$$

$$n=23 \qquad S_{xy}=23.9 \qquad R^2=0.89 \tag{5}$$

Finally, using multiple regression, we predicted (adj $R^2 = 0.83$, $P < 0.001$) species richness in the 100-m^2 plot of the Modified-Whittaker and Intensive plots using species richness at 1-m^2 plots and other ancillary data; the standard error of the coefficients appears below each coefficient:

$$\text{Species in } 100\text{ m}^2=\underset{(199.9)}{766.351}+\underset{(0.226)}{2.43}\times\text{species in } 1\text{ m}^2-\underset{(<0.001)}{0.002}\times\text{UTMx}-\underset{(0.016)}{0.031}\times\text{aspect}$$

$$n=23 \qquad S_{xy}=3.7 \qquad R^2=0.85 \tag{6}$$

Aspen stand structure and regeneration

All of the Modified-Whittaker plots contained some aspen regeneration, 63% of the Intensive plots contained some regeneration, and 50% of the Extensive plots contained regeneration (Table 4).

Discussion

Managers of both public and private land may not have sufficient time or funds to adequately describe patterns of plant diversity throughout the landscape with an abundance of large, multi-scale plots (Tables 1 and 2). Alternatively, simple-small plots may require less time to measure, but may not adequately represent landscape condition (Tables 1 and 2; Stohlgren et al. 1998a), or be an efficient way to capture plant species richness. Combining these alternatives in a single inventory effort

Table 4. The characteristics of the aspen stand structure as sampled with the nested-intensity sampling design in the Sangre de Cristo mountains of Colorado.

	Modified-Whittaker plot (1000 m^2)	Intensive plot (100 m^2)	Extensive plot (100 m^2)
Number of plots			
With >2 m tall, <10 cm dbh	8	11	18
Without >2 m tall, <10 cm dbh	0	4	9
Total	8	15	27
Mean stems/ha[a]			
>10 cm dbh	1125 (320.6)	867 (180.7)	941 (118.8)
<10 cm dbh	1675 (549.0)	1027 (270.4)	1237 (243.4)
Minimum stems/ha[a]			
<10 cm dbh	400	0	0
Maximum stems/ha[a]			
<10 cm dbh	4800	2800	4000

[a]Stems >2 m tall.

leverages the advantages of different plot types, provides insight into the effect of plot size on inventory efforts, and may be an efficient means for increasing inventory quality and usefulness.

Advantages and disadvantages of the three designs

The vegetation sampling techniques described in this study possessed specific advantages and disadvantages. The methods differed in their ability to accurately quantify local and landscape-scale patterns of plant richness and cover, species–area curves, and aspen stand structure. However, the use of all three plot designs frequently allowed the advantages of one design to account for the disadvantages of another plot design.

The Modified-Whittaker design quantified species richness and cover with greater accuracy and efficiency than the other designs. It captured greater species richness per plot than the other two techniques (Table 2), and cumulatively the Modified-Whittaker design detected more unique species than the other two designs (Table 2). Furthermore, the Modified-Whittaker plot accumulated species at a faster rate than other designs (Figure 2), and the large plot of 1000 m^2 accounted for 14 of the 30 unique species, and two of these were unique exotic species. These results emphasize the ability of the larger plot size to detect locally rare and patchy species not captured in small plots.

The four sample scales nested within the large Modified-Whittaker plot insure accurate species–area relationships that describe local diversity. The slope of the species–area curve built from the three scales of the Intensive design suggested that the number of species in the 1000-m^2 plot of the Modified-Whittaker plot could be estimated with the Intensive plot data. However, using the Modified-Whittaker plot remains important, as the Intensive plot could predict richness but not the identity of those extra species captured by the Modified-Whittaker technique. Not only was the

Modified-Whittaker plot able to add two unique exotic species to the total species list, in both cases the exotic species were only detected in the 1000-m^2 plot. This re-emphasizes that the large plot size is necessary for the early detection of exotic plant invasion and the presence of patchily distributed and locally rare species (Stohlgren et al. 1998a; this study).

The Modified-Whittaker sustained disadvantages as well. The design is expensive and time consuming. The cost associated with the Modified-Whittaker might limit the number of plots, thus increasing the probability of missing important locations across the landscape, reducing the environmental gradient sampled, and making extrapolation to unsampled areas difficult. Furthermore, expense and time limitations might limit the frequency of resampling sites, thus sacrificing the early detection of vegetation trends (Stohlgren 1994).

The smaller size and fewer subplots of the Intensive plot allowed many Intensive plots to be distributed across the study area for a cost (sample and travel time; Table 1) similar to the Modified-Whittaker plots. The greater number of plots facilitated better coverage of complex environmental gradients (Figure 4), and a greater chance of locating rare microhabitats that host unique species. Despite the effort to account for landscape-scale variation with a greater number of plots, the Intensive plot design maintained multi-scale sampling features that allowed for calculation of species cover as well as richness. These features also facilitated species richness characterizations with species–area curves at Extensive sample locations (Figure 5, Appendix 1), and made the Intensive design effective for calibrating other sampling techniques. For example, the Intensive design increased the accuracy of the species–area curves developed to describe the sampled aspen vegetation by sampling at many points. The choice of the species–area curve model, and multi-scale extrapolations to the single-scale Extensive plot data may have been less accurate if formulated on the data from the eight Modified-Whittaker plots alone.

The exclusion of 1000-m^2 measurements caused most of the disadvantages associated with the Intensive plot. The Intensive plot captured fewer species per plot (Table 2) and fewer unique species (Table 2) than the larger Modified-Whittaker plot. Decreasing the number of subplots may have reduced the accuracy of the curve used to describe diversity at particular locations and across the entire vegetation type. Furthermore, maintaining the multi-scale component still required significant sampling time and therefore limited the number of plots and landscape-scale heterogeneity sampled.

The Extensive plot, also characterized by the 100-m^2 plot but without nested subplots, increased the ability of this study to account for a large degree of spatial heterogeneity across the landscape (Figure 4). The inclusion of this design added one exotic species to the total species list (Table 2), added additional patches of aspen regeneration (Table 4), and established a landscape-scale baseline of data suitable for detecting early and isolated change in the landscape. A greater number of monitoring locations will be more likely to detect localized disturbance or exotic plant invasion, as processes that influence change may have patchy effects (Baker 1989; Green 1989; Turner 1989). We were able to increase the value of these widely

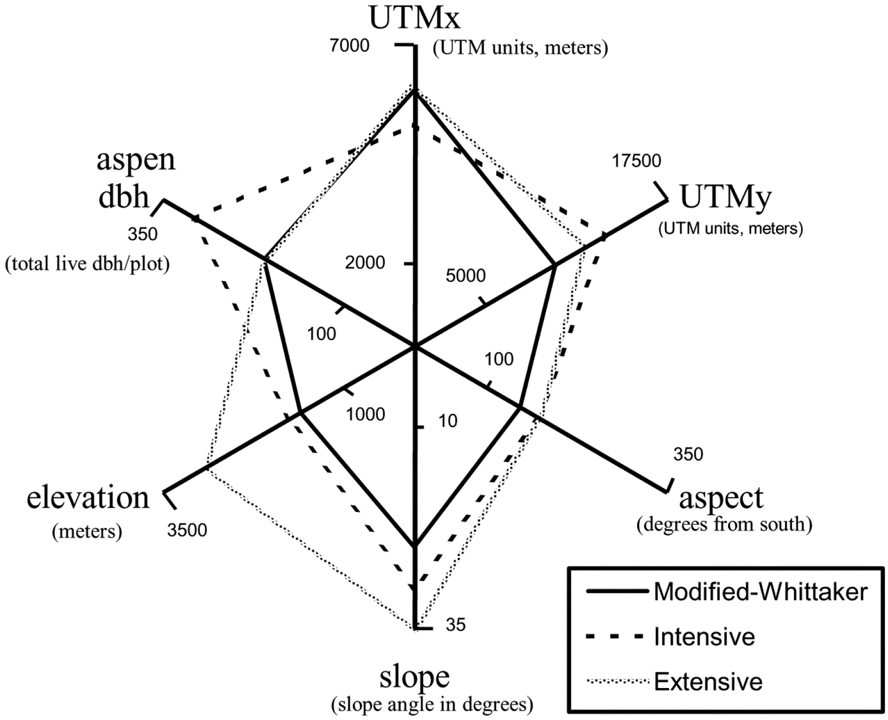

Figure 4. The difference between the minimum and maximum values of the environmental variables provides an estimate of the environmental gradient accounted for by the respective plot designs. Larger values on an axis are indicative of greater heterogeneity sampled by a particular plot design.

distributed Extensive plot data. Because the simplified data were similar to the data collected at the multi-scale plots, statistical models developed using the data from Modified-Whittaker and Intensive plots were able to estimate some of the information not collected at the Extensive plots.

The Extensive plot also had disadvantages. The smaller size of the plot missed species at sample points (Table 2), thus limiting accuracy, and captured fewer unique species than the larger Modified-Whittaker design (Table 2). With no 1-m^2 subplots, species cover could not be recorded in the Extensive plots. Simply collecting the number and identity of species does not provide cover estimates necessary for detecting species-specific increase or decline. For example, assessing changes in cover of the exotic species, *Poa pratensis*, in a particular plot and across many plots may alert managers to the site-specific spread of the exotic species.

Eliminating the subplots from the Extensive design limited the measure of species richness to a single scale and provided little insight into species–area relationships. This exception limits the usefulness of the information collected at each location, especially when compared to other plot locations that describe species richness at a variety of scales. Finally, collecting less information at a specific location increased

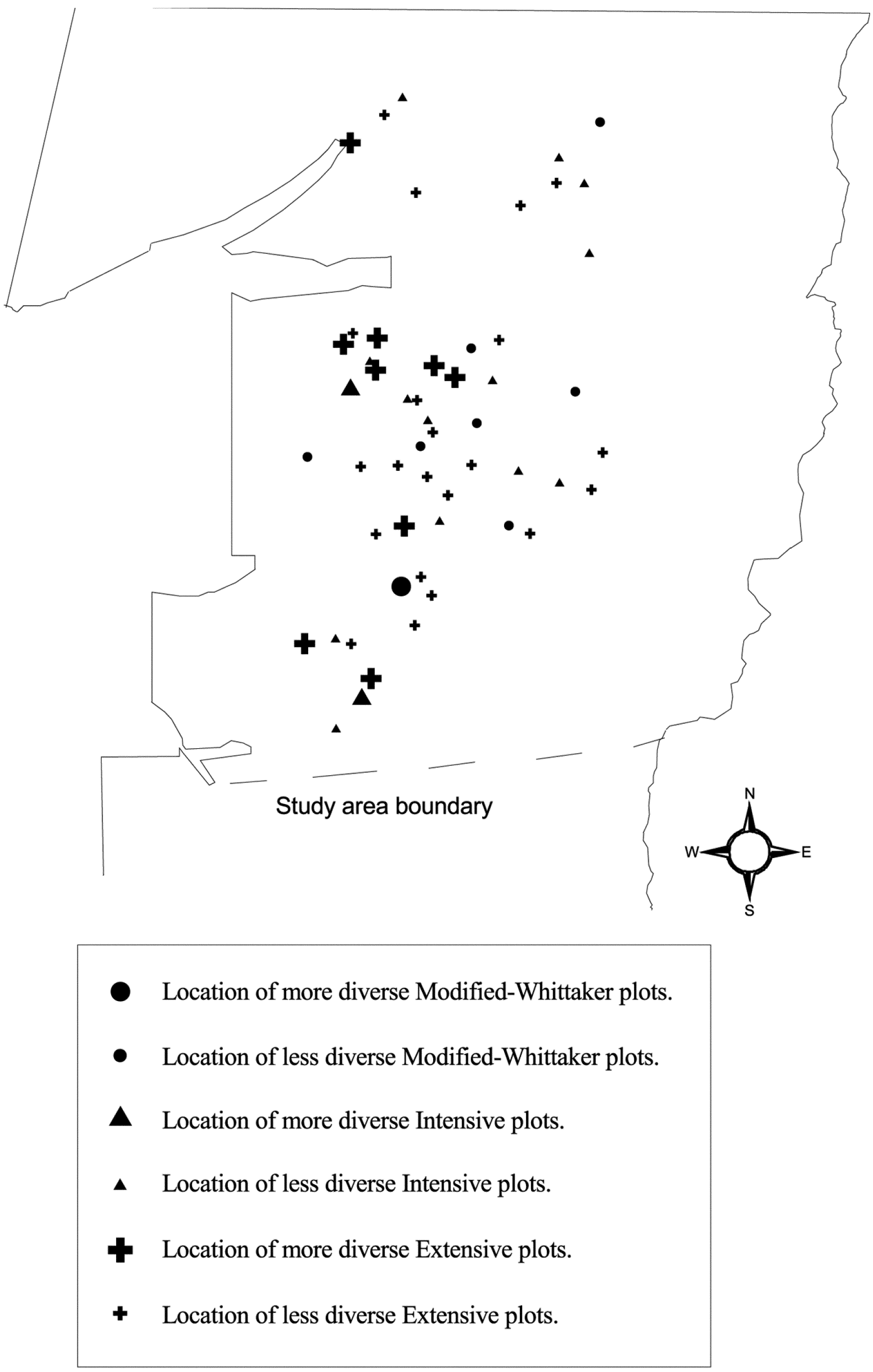

Figure 5. The location of all the plots sampled. Twelve locations, identified by the larger symbols, indicate the most diverse plots.

the cost of travel time and therefore the cost for the information return at a local point.

Benefits of the nested-intensity design

While each of the sampling designs offered unique disadvantages to a more comprehensive (and unaffordable) inventory effort, the advantages of one design often addressed the shortcomings of another design. The nested-intensity design applied all three methods to leverage the advantages of the three designs, allowing for an increase in sample size while efficiently collecting high quality and useful data at a variety of scales.

Combining the advantages of the three plot types addressed the previously discussed trade-offs faced by so many inventories.

(1) *Quality information at localized points may sacrifice understanding of landscape patterns*. The ability of the Modified-Whittaker to accurately describe local species richness, detect unique species, and formulate accurate species–area curves provided quality descriptions at local scales. The smaller, more numerous plot types of the nested-intensity design evaluated landscape-scale patterns perhaps missed by the Modified-Whittaker plots.

(2) *Spatial extent is increased at the expense of detailed understanding at local scales*. The smaller size and less rigorous protocol of the Intensive and Extensive plot designs allowed us to increase the spatial extent of the inventory. With the Intensive plots we nearly doubled the number of Modified-Whittaker plots on the landscape for the same cost, while maintaining the ability to quantify cover and create species–area curves. The Extensive plots further increased the extent of the study, but the large number of plots limited sampling to one scale with no evaluation species cover.

(3) *Intricate methods for inventory are often not used by managers due to their complexity*. A variety of designs with simple alternatives make collection of some information available to managers with limited funding or taxonomic skill. Used together, the three designs provide a technique for assessing a range of patterns of diversity in complex landscapes that are cost-effective and information rich at a variety of scales.

The advantages of the Modified-Whittaker (Table 2; Stohlgren et al. 1998a, b, 1999, 2000) sampling design to quantify plant species diversity at landscape scales might prompt managers to assess landscape patterns of plant diversity only using a large and multi-scale design. If we dedicated all the funding and time available for this inventory effort to sampling with Modified-Whittaker plots, approximately 24 plots could have been placed on the landscape. Given the steep Modified-Whittaker species–accumulation curve (Figure 2), 24 Modified-Whittaker plots may have been the best option if simply generating the largest plot-based species list was the inventory objective. However, most managers must consider entire landscapes. The increased sample of 51 plots using all three sample designs may provide a more complete picture of landscape condition and variation, especially if the data collected at the less small and single-scale plots can be leveraged as with traditional double sampling techniques.

Similar to double sampling techniques, we leveraged the study design by relating data collected with fast and simple designs to more detailed data. We demonstrated the power of the nested-intensity design by detecting hot spots of species richness across the aspen landscape. Using a multiple regression model parameterized with data from the multiple-scale Modified-Whittaker and Intensive plots, we estimated species–area curves for each Extensive plot location (Appendix 1). Generation of species–area curves for every location allowed each plot to be ranked and spatially mapped according to the steepness of the slope or the richness at each location (Figure 5). Species richness may vary across scales (Gaston 2000), so the slope of a curve is a powerful tool for detecting local hot spots of diversity (Connor and McCoy 1979; Rosenzweig 1995; Stohlgren et al. 1997b). Detection of hot spots of diversity on the landscape may be important for setting priorities for preservation of important habitats or landscapes (Margules and Pressey 2000; Myers et al. 2000), directing management activities (Nusser and Goebel 1997; Mulder et al. 1999), or locating regions or plots important for inventory and monitoring purposes (Stohlgren et al. 1997c, 2000).

Numerous possibilities exist for leveraging the effectiveness of a nested-intensity design. For example, we used the nested-intensity approach to evaluate the spatial distribution of successful aspen regeneration. We collected more detail on stand structure at the Modified-Whittaker and Intensive plots than the Extensive plots, but the quantity of pole-like stems indicative of recent regeneration was recorded in all plots. Using methods similar to the species richness predictions, we were able to estimate the diameter of live and dead stems in Extensive plots (Equation 5). Similar manipulations could be attempted to increase the spatial understanding of aspen stand structure and regeneration for both baseline inventory and monitoring purposes. Alternatively, a manager not concerned with patchy processes such as herbivory and fire, which affect the spatial distribution of aspen regeneration (Romme et al. 1995), might simply be interested in the average number of regenerating stems on a landscape. This question may not require a large sample size facilitated by the nested-intensity design, as Monte Carlo simulations suggested that only 10–15 plots would be needed to indicate that there was an average of approximately 1300 regenerating stems per hectare on this landscape. The ability of nested-intensity techniques to evaluate the condition of aspen demonstrates that such a system can be used to address a variety of taxonomic species, but may not be necessary in all cases.

Assessing cumulative species in an area: lessons learned

Examination of species–accumulation curves allowed us to further evaluate the contribution of each sampling design to the nested-intensity design. The steeper curve of the Modified-Whittaker design (Figure 2) indicated that these plots accumulated species at a faster rate than the other designs, and reflects the ability of the larger Modified-Whittaker plot to detect more species per plot than the smaller designs (Table 2). The Intensive plots accrued a species–accumulation curve steeper than the Extensive plots (Figure 2). This difference must be caused by greater species diversity at some of the locations where the Intensive plots were sampled, as the Intensive and Extensive plots were the same size. We expect that the trajectory of these curves would become quite similar with continued sampling, which would extend the curves and dampen the effect of hot spots of diversity on the landscape.

The attributes of a plot cannot be assessed by plot size alone. The contribution of each plot design can be compared by quantity and the quality or usefulness of information returned for the total effort of sampling with that design. The Extensive plots do not contain subplots for collecting estimates of species cover essential for tracking information, such as the spread of exotic species or the progress of restoration efforts. This omission makes the Extensive plots quicker to sample but far less useful to managers. The Modified-Whittaker and Intensive plots must be used if managers require cover estimates of the species detected. Sampling the Modified-Whittaker and Intensive plots required similar effort, approximating a ratio that allows just fewer than two Intensive plots to be placed on the landscape for every one Modified-Whittaker plot (Table 1). With similar effort, the eight Modified-Whitaker plots provided greater species richness and cover for more species than the 15 Intensive plots (Tables 1 and 2). The quality and quantity of information provided by the Modified-Whitaker dispels the popular notion that many small plots are more effective than a few large plots.

The species–accumulation curves that describe the contribution of each plot type to the total species detected elucidates the bias of the smaller plot sizes (Figure 3). The flattening of the sections of the curve contributed by both the Intensive and Extensive plots suggests that further sampling would detect few new species. However, regardless of the order included, the steep curve defined by the Modified-Whittaker plots indicates that these large plots detect species missed by the smaller plots (Figure 3). The underestimation of species richness resulting from small plot sampling produces a less accurate and less complete inventory with which to guide management. In fact, if a manager were to iteratively assess the degree of completeness of an inventory either with statistical techniques (see Bunge and Fitzpatrick 1993; Schreuder et al. 1999) or looking at the slope of the species accumulation curve, the inventory might be halted prematurely if sampling were only conducted with plots even of the 100-m^2 size.

Other management applications

Managers could adopt this nested-intensity sampling strategy to efficiently address time, funding, and spatial and temporal accuracy concerns. For example, pilot studies (Ludwig and Reynolds 1988; Krebs 1989; Reed et al. 1993) have long been recommended for determination of sample size. The number of study plots required to account for variability may often be underestimated, as the small number of pilot plots may not sample enough locations to accurately describe the environmental variability across the study area. The use of this nested-intensity design may help an investigator better understand the extent of the variation on the landscape, without the cost and time associated with the inclusion of many detailed plots on the landscape. The number of plots and the proportion of the techniques used depend on the landscape, the number of vegetation types and rare habitats, questions of interest to managers, and time and money available for the work. The inventory must be an iterative process with the number and location of plots informed and directed by the data collected.

The nested-intensity design could contribute to this iterative approach. The number of species in an Extensive plot, or the predicted species–area curve for that plot, might indicate that the plot location is import to managers, perhaps due to high species richness or because of the presence of a particular exotic species. Such an area may require monitoring efforts more frequently than areas of less interest. The information obtained from Extensive plots may even lead a manager to place a Modified-Whittaker or Intensive plot at that location in future monitoring efforts, to gain greater detail about species cover at finer scales, and species composition at larger scales.

Managers with access to computer and statistical expertise can use spatial models to predict species distributions across the landscape to continue to improve their inventory programs. Models applied to multi-scale plant species data (Reich and Bravo 1998; Chong et al. 2001) use spatially explicit tools to describe the distribution of native and exotic species. The Extensive plots used in this design would provide a means for improving and testing the accuracy of such maps without the expense of placing many new large plots on the landscape.

Those managers who may not have adequate funding or scientific expertise to pursue such a thorough inventory system may also benefit from the nested-intensity design. Simplified monitoring could be practiced between periodic intensive investigations, creating a nesting of knowledge and time. The ability of a manager to predict the number of species in a 100-m^2 plot with data from 1 m^2 is just one example (Equation 6). Managers who do not have extensive taxonomy skills could simply count the number of different morphological species (based on different appearance) in Extensive plots to identify hot spots for later detailed research by trained taxonomists. A manager could learn to identify a small number of species and search Extensive plots or even the 100-m^2 plot of a Modified-Whittaker plot. For instance, we found the easily identified and highly competitive exotic grass *Bromus inermis* at several plots. If a manager learned this species and could quantify its spread, the resulting data could direct control efforts. A manager could also learn to identify exotics thus far undetected on the landscape, such as field bindweed (*Convolvulus arvensis*). Early detection of this species would ease control efforts. Managers could also repeatedly measure just the 1-m^2 subplots of a Modified-Whittaker or Intensive plot for the cover of such species in an effort to track subtle changes over time. An initial nested-intensity inventory could direct managers to important locations for monitoring (Stohlgren et al. 1997b). The data obtained from the abridged monitoring with 1-m^2 or Extensive plots could not only direct management, but also register thresholds that suggest the need for another intensive inquiry with Modified-Whittaker and Intensive plots.

Conclusions

The principles of the nested-intensity inventory method described here could be adapted for use in any landscape, and to address a variety of management questions. Exploration of the methods used in this study demonstrated several benefits to inventory programs:

- The nested-intensity design accounted for local and landscape variability, while increasing time efficiency and reducing costs;
- The large size of the Modified-Whittaker plot captured greater species richness per plot and more unique species than smaller plot-size methods;
- The Intensive plot increased the spatial extent of the study and increased the accuracy of species–area curves that defined the vegetation type;
- The Extensive plot further increased the landscape-scale heterogeneity sampled, adding unique species and locating hot spots of diversity and additional patches of aspen regeneration.

This nested-intensity system should make sound inventory techniques available to managers of both public and private land, and could increase the effectiveness and spatial extent of established monitoring programs.

Acknowledgements

Geneva Chong, Michelle Lee, and Greg Newman contributed valuable ideas and/or editorial comments. Cindy Villa, Rick Shory, Annie Overlin, and Lisa Schell provided invaluable help with field work and taxonomic advice. Tom Wolf and Karl Hess helped establish the inventory effort, Vic White provided advice on road and trail access and vehicle support. Comments from anonymous reviewers greatly improved the manuscript. Logistical support was provided by the US Geological Survey Global Change Research Program and the Natural Resource Ecology Laboratory at Colorado State University. To all we are incredibly grateful.

Appendix 1

The intercept, measured slope of the species−log area curves, and the predicted slope of the species−area curve at vegetation plots in southern Colorado.

Plot	Intercept	Measured slope	Predicted slope
Modified-Whittaker			
1	0.882	0.297	0.316
2	1.086	0.196	0.223
3	1.033	0.223	0.214
4	0.807	0.255	0.234
5	0.774	0.352	0.289
6	1.084	0.222	0.224
7	1.132	0.217	0.231
8	1.082	0.216	0.204
Intensive			
1	1.087	0.221	0.238
2	0.745	0.310	0.291
3	0.911	0.220	0.208
4	0.570	0.341	0.365
5	1.097	0.229	0.256
6	1.092	0.279	0.234
7	1.275	0.204	0.215
8	1.025	0.255	0.275
9	1.012	0.213	0.233
10	0.780	0.222	0.254
11	0.674	0.313	0.281
12	1.263	0.196	0.271
13	1.082	0.218	0.208
14	0.621	0.289	0.263
15	1.102	0.211	0.228
Extensive			
1			0.303
2			0.290
3			0.294
5			0.284
6			0.300
7			0.277
8			0.290
9			0.227
10			0.247
11			0.295
12			0.232
13			0.324
14			0.300
15			0.259
16			0.344
17			0.252
18			0.289
19			0.266
20			0.282
21			0.264
22			0.252
23			0.241
24			0.248
25			0.269
26			0.295
27			0.290
28			0.222

References

Baker W.L. 1989. Landscape ecology and nature preserve design in the boundary waters canoe area, Minnesota. Ecology 70: 23–35.

Baker W.L., Munroe J.A. and Hessl A.E. 1997. The effects of elk on aspen in the winter range of Rocky Mountain National Park. Ecography 20: 155–165.

Bonham C.D. 1989. Measurement for Terrestrial Vegetation. John Wiley and Sons Inc., New York.

Bunge J. and Fitzpatrick M. 1993. Estimating the number of species: a review. Journal of the American Statistical Association 88: 364–373.

Burnham K.P. and Anderson D.R. 1998. Model Selection and Inference: A Practical Information – Theoretic Approach. Springer-Verlag, New York.

Chong G.W., Reich R.M., Kalkhan M.A. and Stohlgren T.J. 2001. New approaches for sampling and modeling native and exotic plant species richness. Great Basin Naturalist 61: 328–335.

Colwell R.K. 1997. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 5. User's Guide and Application. Published at: http://viceroy.eeb.uconn.edu/estimate.

Connor E.F. and McCoy E.D. 1979. The statistics and biology of the species–area relationship. The American Naturalist 113: 791–833.

Daubenmire R.F. 1959. Canopy coverage method of vegetation analysis. Northwest Science 33: 43–64.

DeByle N.V. 1985. Wildlife. In: DeByle N.V. and Winokur R.P. (eds), Aspen: Ecology and Management in the Western United States. General Technical Report RM-119. USDA Forest Service, Fort Collins, Colorado pp. 135–152.

Flather C.H. 1996. Fitting species–accumulation functions and assessing regional land use impacts on avian diversity. Journal of Biogeography 23: 155–168.

Gaston K.J. 2000. Global patterns in biodiversity. Nature 405: 220–227.

Green D.G. 1989. Simulated effects of fire, dispersal, and spatial pattern on competition within forested mosaics. Vegetatio 82: 139–153.

Harte J., Kinzig A. and Green J. 1999. Self-similarity in the distribution and abundance of species. Science 284: 334–336.

Kalkhan M.A., Reich R.M. and Stohlgren T.J. 1998. Assessing the accuracy of Landsat Thematic Mapper classification using double sampling. International Journal of Remote Sensing 19: 2049–2060.

Kotliar N.B. 1996. Scale dependency and the expression of hierarchical structure in Delphinium patches. Vegetatio 127: 117–128.

Krebill R.G. 1972. Mortality of aspen on the Gros Ventre Elk Winter Range. USDA Forest Service Research Paper INT-129. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Krebs C.J. 1989. Ecological Methodology. Harper & Row, New York.

Leitner W.A. and Rosenzweig M.L. 1997. Nested species–area curves and stochastic sampling: a new theory. Oikos 79: 503–512.

Levin S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.

Ludwig J.A. and Reynolds J.F. 1988. Statistical Ecology. John Wiley & Sons Inc., New York.

Margules C.R. and Pressey R.L. 2000. Systematic conservation planning. Nature 405: 243–253.

MathSoft Inc. 1999. S-Plus 2000. MathSoft Inc., Seattle, Washington.

Mulder B.S., Noon B.R., Spies T.A., Raphael M.G., Palmer C.J., Olsen A.R. et al., 1999. The strategy and design for the effectiveness monitoring program for the Northwest Forest Plan. General Technical Report PNW-GTR-437. USDA National Forest Service, Portland, Oregon.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. and Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nusser S.M. and Goebel J.J. 1997. The National Resources Inventory: a long-term multi-resource monitoring programme. Environmental and Ecological Systematics 4: 181–204.

Parker K.W. 1951. A Method for Measuring Trend in Range Condition in National Forest Ranges. USDA National Forest Service, Washington, DC.

Peterson D.L., Silsbee D.G. and Schmoldt D.L. 1995. A planning approach for developing inventory and monitoring programs in national parks. Natural Resources Report NPS/NRUW/NRR-95/16. National Park Service, Washington, DC.

Reed R.A., Peet R.K., Palmer M.W. and White P.S. 1993. Scale dependence of vegetation–environment correlations: a case study of a North Carolina piedmont woodland. Journal of Vegetation Science 4: 329–340.

Reich R.L. and David R. 1998. Quantitative Spatial Analysis. Colorado State University, Fort Collins, Colorado, www.CNR.colostate.edu/~robin.

Reich and Bravo 1998. Integrating spatial statistics with GIS and remote sensing in designing multi-resource inventories The North American Symposium Towards a Unified Framework for Inventory and Monitoring Forest Ecosystem Resources. Guadalajara, Mexico.

Ripple W.J. and Larsen E.J. 2000. Historic aspen recruitment, elk, and wolves in Northern Yellowstone National Park, USA. Biological Conservation 95: 361–370.

Romme W.H., Turner M.G., Wallace L.L. and Walker J.S. 1995. Aspen, elk, and fire in Northern Yellowstone National Park. Ecology 76: 2097–2106.

Rosenzweig M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

SAS Institute 1998. SAS for Windows. SAS Institute, Cary, North Carolina.

Schreuder H.T., Williams M.S. and Reich R.M. 1999. Estimating the number of tree species in a forest community using survey data. Environmental Monitoring and Assessment 56: 293–303.

Shmida A. 1984. Whittaker's plant diversity sampling method. Israel Journal of Botany 33: 41–46.

Simonson S.E., Opler P.A., Stohlgren T.J. and Chong G.W. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation 10: 1369–1386.

SPSS Inc. 2000. SYSTAT 9. SPSS Inc., Chicago, Illinois.

Stohlgren T.J. 1994. Planning long-term vegetation studies at landscape scales. In: Powell T.M. and Steele J.H. (eds), Ecological Time Series. Chapman & Hall, New York, pp. 209–241.

Stohlgren T.J., Binkley D., Chong G.W., Kalkhan M.A., Schell L.D., Bull K.A. et al. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25–46.

Stohlgren T.J., Bull K.A. and Otsuki Y. 1998a. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. Journal of Range Management 51: 164–172.

Stohlgren T.J., Bull K.A., Otsuki Y., Villa C.A. and Lee M. 1998b. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology 138: 113–125.

Stohlgren T.J., Chong G.W., Kalkhan M.A. and Schell L.D. 1997a. Multi-scale sampling of plant diversity: effects of minimum mapping unit size. Ecological Applications 7: 1064–1074.

Stohlgren T.J., Chong G.W., Kalkhan M.A. and Schell L.D. 1997b. Rapid assessment of plant diversity patterns: a methodology for landscapes. Environmental Monitoring and Assessment 48: 25–43.

Stohlgren T.J., Coughenour M.B., Chong G.W., Binkley D., Kalkhan M.A., Schell L.D. et al. 1997c. Landscape analysis of plant diversity. Landscape Ecology 12: 155–170.

Stohlgren T.J., Falkner M.B. and Schell L.D. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio 4: 1–8.

Stohlgren T.J., Owen A. and Lee M. 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. Biodiversity and Conservation 9: 67–86.

Turner M.B. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecological Systematics 20: 171–197.

USDA, NRCS 2001. The PLANTS Database. Version 3.1. National Plant Data Center, Baton Rouge, Louisiana, US, (http://plants.usda.gov).