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A Modified-Whittaker nested vegetation sampling method

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Key words: Nested sampling techniques, Plant species richness, Species-area curves, Species diversity

Abstract

A standardized sampling technique for measuring plant diversity is needed to assist in resource inventories and for monitoring long-term trends in vascular plant species richness. The widely used 'Whittaker plot' (Shmida 1984) collects species richness data at multiple spatial scales, using 1 m², 10 m², and 100 m² subplots within a 20 m × 50 m (1000 m²) plot, but it has three distinct design flaws involving the shape and placement of subplots. We modified and tested a comparable sampling design (Modified-Whittaker plot) that minimizes the problems encountered in the original Whittaker design, while maintaining many of its attractive attributes. We overlaid the two sampling methods in forest and prairie vegetation types in Larimer County, Colorado, USA (n = 13 sites) and Wind Cave National Park, South Dakota, USA (n = 19 sites) and showed that the modified design often returned significantly higher ($p < 0.05$) species richness values in the 1 m², 10 m², and 100 m² subplots. For all plots, except seven ecotone plots, there was a significant difference ($p < 0.001$) between the Whittaker plot and the Modified-Whittaker plot when estimating the total number of species in the 1000 m² plots based on linear regressions of the subplot data: the Whittaker plot method, on average, underestimated plant species richness by 34%. Species-area relationships, using the Modified-Whittaker design, conformed better to published semilog relationships, explaining, on average, 92% of the variation. Using the original Whittaker design, the semilog species-area relationships were not as strong, explaining only 83% of the variation, on average. The Modified-Whittaker plot design may allow for better estimates of mean species cover, analysis of plant diversity patterns at multiple spatial scales, and trend analysis from monitoring a series of strategically-placed, long-term plots.

Introduction

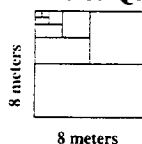
Several recent books have focused on the importance of biological diversity (e.g. Magurran 1988; Wilson 1988; Soulé & Kohm 1989; Peters & Lovejoy 1992), but none contain precise methodologies to measure it. There has been a renewed interest to quantify patterns of biological diversity at state and national scales (e.g. GAP Analysis; Scott *et al.* 1993), and local scales (Dallmeier 1992; Tilman & Downing 1994), but landscape ecologists have not yet agreed on a standardized field methodology for evaluating plant diversity (Stohlgren 1994).

Textbooks on vegetation sampling methods (e.g. Mueller-Dombois & Ellenberg 1974; Barbour *et*

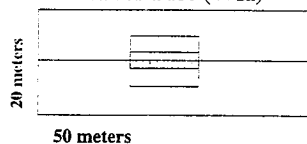
al. 1987) recommend overlaying nested quadrats of increasing size to quantify species-area curves (Fig. 1a) – one measure of species richness in an area. Palmer (1990, 1991) compared several methods for estimating species richness including: number of observed species, extrapolation from species-area curves, integration of the lognormal distribution, and nonparametric estimators. He cautioned that species-area curves may have different forms at different scales. Extrapolation of species-area information may also be influenced by the sampling design used.

We believe many field ecologists continue to agonize about how to select the appropriate quadrat shapes and sizes for particular vegetation types (also see Podani *et al.* 1993). This problem is, of course, magni-

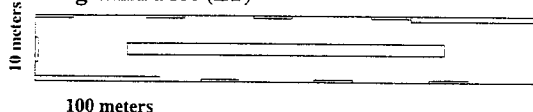
A. Nested Quadrat



B. Whittaker Plot (WH)



C. Long-Thin Plot (LT)



D. Modified-Whittaker Plot (MW)

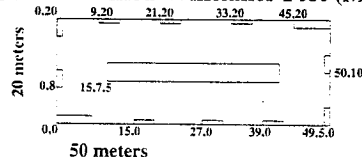


Fig. 1. Nested vegetation sampling designs. (A) Nested Quadrat design (from Mueller-Dombois & Ellenberg 1974), (B) Whittaker Plot design (from Shmida 1984), (C) Long-Thin Plot design (from Stohlgren 1994), and (D) Modified-Whittaker Plot design (this paper; shown with x, y coordinates of subplot and plot corners).

fied when multiple vegetation types or large, heterogeneous landscapes must be studied (Stohlgren 1994).

Shmida (1984) published a nested vegetation sampling method that was developed and used by R. H. Whittaker over many years. The primary purpose of that paper was to present Whittaker's nested vegetation sampling technique for the measurement of species diversity to compare different plant communities from different regions of the world. Whittaker (1977) had long realized that patterns of plant diversity can be elucidated only by systematic surveys and by sampling at multiple spatial scales (i.e. nested quadrat sizes of 1 m², 10 m², and 100 m² within a 1000 m² area). Multi-scale sampling of vegetation allows for: (1) evaluations of the influence of spatial scale on local species richness patterns (Podani *et al.* 1993); (2) better comparisons of community richness than single-scale measurements provide (Whittaker 1977); and (3) the development of species-area (or 'collector's curves'; Pielou 1977) to estimate larger-scale richness patterns (Shmi-

da 1984). Shmida (1984) showed a strong semilog relationship

$$S = b + d \log A \quad (1)$$

between the number of species (S) and quadrat area (A) (b is a constant, d is the slope). This is similar to other reported species-area relationships (Miller & Wiegert 1989; Shafer 1990; but see Pielou 1977).

The 20 m × 50 m size of the 'Whittaker plot' (Fig. 1b) was designed initially for more-or-less homogeneous areas so that replicate sites were easy to find (Shmida 1984). Borrowing perhaps from the nested quadrat approach (Fig. 1a), the 1 m × 1 m subplots are overlaid on the 2 m × 5 m subplots, which, in turn, are overlaid on the 10 m × 10 m subplot. The most attractive attributes of the Whittaker plot design are that it provided plant ecologists with: (1) a standardized approach to quantify species richness in different plant communities; and (2) insights on the effects of quadrat size when determining species-area relationships.

Stohlgren (1994) pointed out that the Whittaker plot has three distinct design flaws. First, if the habitat is not strictly homogeneous, species richness is influenced by plot shape. Circular or square plots (with a reduced perimeter to surface area ratio) will have fewer species, in general, than a long-thin rectangle covering a more heterogeneous area (Bormann 1953). Second, plot size and shape interactions may influence species richness (Pielou 1977). Note that the Whittaker plot design shifts from 1 m × 1 m squares to 2 m × 5 m rectangles to a 10 m × 10 m square, then back to a 20 m × 50 m rectangle, which confounds the influences of plot shape and size (Table 1; Fig. 1b). Third, is the problem of spatial autocorrelation. Not only are the ten 1 m × 1 m plots contiguous in one small area of the 20 m × 50 m plot (i.e. high spatial autocorrelation), the successively larger plots are superimposed on the smaller plots (i.e. the plots are not independent in terms of species richness). Thus, a species-rich area in one of the 1 m × 1 m plots affects the species richness reported in the larger-sized plots. This last problem is inevitable among nested (overlaid) quadrats (e.g. Mueller-Dombois & Ellenberg 1974; Pielou 1977; Barbour *et al.* 1987), and results may be heavily biased by the starting location in the field.

Initiated in May, 1992, the primary objective of our vascular plant species richness project was to develop and test alternate field methods to minimize the design problems of the Whittaker plot when collecting plant diversity information. In an earlier study, Stohlgren

Table 1. Dimensions of plots and subplots in various nested vegetation sampling designs.

Dimensions	Design		
	Whittaker	Long-Thin	Modified-Whittaker
Ten 1 m ² subplots	1 m × 1 m (contiguous, clustered)	0.32 m × 3.16 m (systematic, outer perimeter not contiguous)	0.5 m × 2 m (systematic, outer perimeter not contiguous)
Two 10 m ² subplots	2 m × 5 m (contiguous, overlapping)	1 m × 10 m (systematic, outer perimeter non-overlapping)	2 m × 5 m (systematic, outer perimeter non-overlapping)
One 100 m ² subplot	10 m × 10 m (overlapping)	3.16 m × 31.6 m (centered, non-overlapping)	5 m × 20 m (centered, non-overlapping)
One 1000 m ² plot	20 m × 50 m (overlapping)	10 m × 100 m (overlapping)	20 m × 50 m (overlapping)
Source	Shmida 1984	Stohlgren 1994	This paper

(1994) developed and tested an alternate nested vegetation sampling design (10 m × 100 m 'long-thin plot'; Fig. 1c; Table 1) in the Beaver Meadows area of Rocky Mountain National Park, Colorado, USA. The 400 m × 350 m area (elevation 2800 m) contained portions of a riparian meadow and a lodgepole pine-ponderosa pine forest. An ecotone area was subjectively defined as within 100 m of the forest edge to test the different plot designs in heterogeneous areas. We randomly located the southwest corner (of north-south oriented plots) and superimposed three Whittaker plots and three long-thin plots in the meadow, ecotone, and forest areas of the study site.

In all habitat types, and for all plot sizes, the long-thin plot design consistently returned higher species richness values than the Whittaker design. And, the species richness sampling with the long-thin plot design more accurately reflected the total species richness recorded in a complete vascular plant survey of the area (Stohlgren 1994). However, the long-thin design was somewhat cumbersome for field crews, and total species richness was not comparable to Whittaker plot data (Whittaker *et al.* 1979; Naveh & Whittaker 1979) or data collected by many investigators who used 20 m × 50 m plots (e.g. Rice & Westoby 1983; Baker 1990). So, a further modification of the Whittaker plot design was warranted. The objectives of this research were to: (1) develop a new nested vegetation plot design (the Modified-Whittaker plot design) that minimizes the statistical problems of the original Whittaker plot design; (2) compare the two designs in several habitats in terms of multi-scale species richness patterns; and (3) evaluate how data collected using the two designs conforms to established species-area relationship theory.

We hoped to develop a standardized nested plot technique that can be used by plant ecologists for better estimates of local species richness and mean species cover, analysis of plant diversity spatial patterns, and trend analysis from monitoring a series of strategically-placed, long-term plots.

Methods and study areas

We modified the 20 m × 50 m Whittaker plot design keeping the attractive features of the long-thin plot and original Whittaker plot designs (Fig. 1d; Table 1). Like the long-thin plot design, the Modified-Whittaker plot design minimizes the problems in the original Whittaker design by using consistent rectangle proportions in the subplots to remove subplot size-shape interactions (Stohlgren 1994). Like the Whittaker plot design, the Modified-Whittaker plot is 20 m × 50 m. However, like the long-thin plot (Fig. 1c), the 1 m² and 10 m² subplots are arranged systematically inside the perimeter of the 20 m × 50 m plot. Likewise, the 100 m² subplot is centered in the plot. The three subplot sizes are independent and non-overlapping and species richness can be used to construct species-area curves. Pielou (1977) used the term 'collector's curve' where one is trying to casually compile an exhaustive list of species in an area or where nested subplots are independent (non-overlapping). We prefer the term species-area curve to collector's curve because: (1) our three subplot sizes are non-overlapping and independent of each other (and only 13% of the 20 m × 50 m plot is not independent); (2) we focus on precise spatial scale aspects of species richness from subplot data; and (3) it is more commonly used and understood.

We compared the Whittaker and the Modified-Whittaker plot designs by overlaying them in a variety of habitat types in Larimer County, Colorado, USA ($n = 13$ sites), and in Wind Cave National Park, South Dakota, USA ($n = 19$ sites; Appendix). We used the paired t test (Zar 1974) to compare the number of species recorded in the 1 m², 10 m², and 100 m² subplots of both plot designs.

We used the semilog expression discussed earlier (i.e. linear regression) to estimate the total number of species in each 1000 m² plot based on the cumulative species recorded in the 1 m², 10 m², and 100 m² subplots. These 'expected' values for both plot designs can be compared to 'observed' values of the total number of species recorded in 20 m \times 50 m plots. Since the observed values were identical for each pair of plots, the paired t test was used to compare the mean observed-expected values for both plot techniques. The plot technique with the smallest differences between observed and expected values would be more useful in estimating local species richness. We also used the semilog linear regressions to evaluate which sampling design conformed better with established species-area relationship theory (Shmida 1984; Shafer 1990). The technique that produced higher coefficients of determination (r^2 values) would be more accurate in estimating the species richness of larger areas (in the same habitat). The paired t test was used to compare mean coefficients of determination of species-area regressions for the different sites and vegetation types.

Results

The Modified-Whittaker plot design returned significantly higher ($p < 0.05$) species richness values in the 1 m², 10 m², and 100 m² subplots for the combined data (Fig. 2). Comparisons of the Whittaker and Modified-Whittaker plot designs also show similar patterns across study sites and in a variety of habitats (Fig. 2). The forest plots were more variable, but still showed the same general pattern.

Species richness in the vegetation communities tested ranged from 10 species/0.1 ha to 69 species/0.1 ha. Based on the semilog linear relationships from the 1 m², 10 m², and 100 m² subplots, we found significant differences between observed and expected values of the total number of species recorded in 20 m \times 50 m plots for all sites and vegetation types (Table 2). With the exception of seven 'ecotone' plots, the Modified-Whittaker plot design was superior to the original

Whittaker plot design for estimating total species richness in the 0.1 ha plots from subplot data.

Using data from the 1 m², 10 m², and 100 m² subplots and 1000 m² plots, we found that the Modified-Whittaker design conformed better to published semilog relationships, explaining, on average, 92% of the variation (Table 3). Using the original Whittaker design, the semilog species-area relationships were not as strong, explaining only 83% of the variation on average. The mean coefficients of determination were significantly different for all sites and vegetation types (except the ecotone plots, which followed the same general pattern but were more variable). Thus, the Modified-Whittaker plot technique was robust across the range of habitats, vegetation types, and land use characteristics included in this study (Fig. 2, Tables 2 and 3, and Appendix) and study plots were lumped for the comparisons that follow.

Based on the semilog linear relationships from the subplots, the Whittaker plot design, on average, underestimated species richness in the 0.1 ha plot by about 34%. The Modified-Whittaker plot design also underestimated total species richness, but only by an average of 9%. The Modified-Whittaker plot design was more stable over the range of species richness values tested (Fig. 3). The Whittaker plot design became less stable (i.e. greater absolute differences between observed and expected values) as plot species richness increased.

Fitting average species richness values from all subplots and plots (Fig. 4), we found a stronger species(S)-area(A ; m²) relationship ($S = 25.5 + 4.5 \times \log A$; $r^2 = 0.992$; $p < 0.0001$) using the Modified-Whittaker design compared to the original Whittaker design ($S = 13.6 + 7.4 \times \log A$; $r^2 = 0.912$; $p < 0.0001$).

Discussion

While additional field tests are needed in other vegetation types, the Modified-Whittaker nested vegetation sampling design looks promising for several reasons. First, the new design minimizes the problems in the original Whittaker design. The consistent rectangle proportions remove subplot size-shape interactions, and rectangles generally perform better than squares at recovering species richness (Stohlgren 1994). The subplots in the Modified-Whittaker design have less overlap than the subplots in the original design (except for the largest size plot, of course). Thus, they are influenced less by spatial autocorrelation and non-

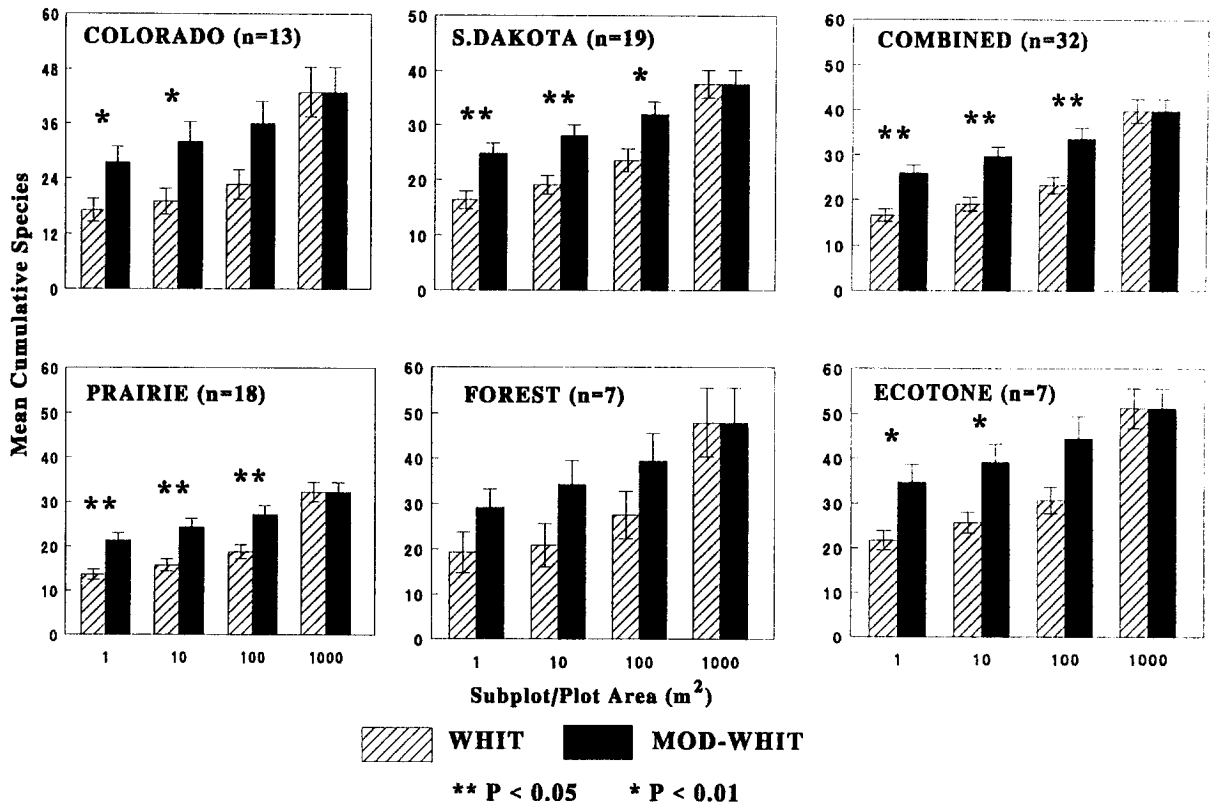


Fig. 2. Comparison of the mean number of species recorded by subplot/plot area in the Whittaker and Modified-Whittaker plot designs for different study locations and vegetation types. Vertical bars represent standard errors. Double asterisks show statistical significant differences at $\alpha = 0.05$ (paired *t* test), a single asterisk denotes a difference at $\alpha = 0.10$.

Table 2. Mean observed-expected species richness values (absolute values) for the 20 m \times 50 m plots.

Site/Vegetation Type	Observed-Expected Species Richness		Paired <i>t</i> test <i>p</i>
	Whittaker Mean (S.E.)	Modified-Whittaker Mean (S.E.)	
Colorado Sites (n = 13)	18.8 (2.6)	3.6 (0.8)	< 0.001
South Dakota Sites (n = 19)	10.6 (1.2)	3.7 (0.7)	< 0.001
Combined Sites (n = 32)	14.0 (1.4)	3.6 (0.5)	< 0.001
Prairie Plots (n = 18)	11.0 (1.4)	3.4 (0.6)	< 0.001
Forest Plots (n = 7)	17.1 (2.3)	4.3 (1.4)	< 0.001
Ecotone Plots (n = 7)	18.3 (4.6)	3.7 (1.3)	< 0.1

independence of observations (Pielou 1977). Because vegetation is often clustered spatially (Fortin *et al.* 1989), and most species are rare in cover and abundance (Barbour *et al.* 1987), the ten contiguous 1 m² subplots in the original Whittaker design are more likely to miss important patches of vegetation and under-

represent small-scale species richness in the 20 m \times 50 m plot. This is precisely what our data show.

The greatest difference in the two techniques is in the number of species recorded in the 1 m² subplots (Fig. 2; Fig. 4). The 1 m² subplots using the Modified-Whittaker design averaged 26.0 (± 1.8 ; S.E.) species,

Table 3. Mean coefficients of determination (r^2) for semilog linear regressions of species (number of species) to area (m^2) relationships. n.s. = not significant.

Site/Vegetation Type	Mean Species-Area r^2		Paired t test p
	Whittaker Mean (S.E.)	Modified-Whittaker Mean (S.E.)	
Colorado Sites (n = 13)	0.785 (0.02)	0.912 (0.02)	< 0.02
South Dakota Sites (n = 19)	0.855 (0.02)	0.922 (0.01)	< 0.05
Combined Sites (n = 32)	0.827 (0.02)	0.917 (0.01)	< 0.01
Prairie Plots (n = 18)	0.820 (0.01)	0.910 (0.02)	< 0.05
Forest Plots (n = 7)	0.820 (0.01)	0.928 (0.02)	< 0.05
Ecotone Plots (n = 7)	0.850 (0.03)	0.927 (0.03)	n.s.

while the Whittaker 1 m^2 subplots averaged only 16.7 (± 1.4) species. The original Whittaker design of contiguous $1\text{ m} \times 1\text{ m}$ subplots (that combined cover only a $1\text{ m} \times 10\text{ m}$ in the center of the $20\text{ m} \times 50\text{ m}$ plot) probably provides a very biased view of small-scale interactions occurring over the plot because the subplots: (1) exclude many species found in the $20\text{ m} \times 50\text{ m}$ plot (Fig. 2); and (2) they result in artificially-low variance due to spatial autocorrelation problems (Stohlgren 1994). Particularly for plant species cover estimates conducted in the 1 m^2 subplots in both designs, the systematic subplots are more likely to give better estimates of mean species cover for the 1000 m^2 area. And, the systematic placement of subplots around the perimeter of the plot allows for the analysis of spatial patterns in plant diversity within a $20\text{ m} \times 50\text{ m}$ area.

Second, the attractive attributes of the original Whittaker design are maintained. A nested vegetation sampling design (i.e. sampling species richness at multiple spatial scales) allows for mathematical estimates of total diversity (Shmida 1984; Palmer 1990, 1991). The same 'sample data sheets' presented in Shmida (1984) can be used. However, species cover-abundance data from the 1 m^2 subplots are improved by recording more species over a broader area of 0.1 ha plot. Strong species-area relationships (Table 3, Fig. 4) allow for better estimates of local species richness from a series of plots (although species-area curves may not always fit the semilog form; Pielou 1977). And, comparisons of species richness can be made among community types or throughout the world by Whittaker and others (e.g. Nevah & Whittaker 1979; Rice & Westoby 1983; Baker 1990).

The systematic placement of the subplots makes the design easy to use in the field now and in the future

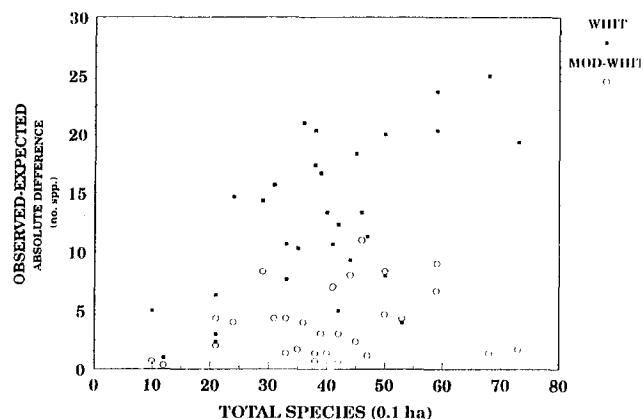


Fig. 3. Relationship of observed minus expected species richness to observed species richness (i.e. total species in each 0.1 ha plot) using the two techniques.

as long-term study plots. Random placement of subplots may produce similar species richness data to the systematic placement used in the Modified-Whittaker design. But, random placement of the non-overlapping subplots (i.e. x , y coordinates, angle, etc.) would be more difficult for field crews, and permanent marking of the subplots would be necessary if trend analysis was a study objective. As stated previously, the long-thin plot design (Fig. 1c) was cumbersome for field crews, and the increased perimeter to area ratio of the subplots made it more difficult for field crews to identify which plants should be included or excluded.

Our botanists outline the $20\text{ m} \times 50\text{ m}$ with two 75 m tapes, use a 50 m tape for the center $5\text{ m} \times 20\text{ m}$ subplot, then use a snap-together $0.5\text{ m} \times 2\text{ m}$ PVC frame to record species cover in the 1 m^2 subplots adjacent to the borders (Fig. 1d). Decimeter markings on the PVC frame aid in the cover estimates. As an inter-

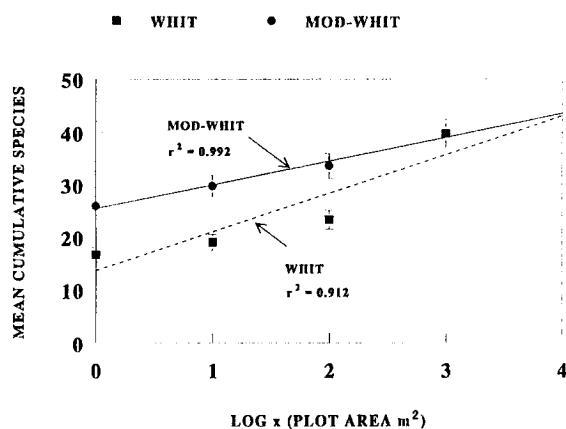


Fig. 4. Overall species-area relationships for the two sampling designs based on the mean number of species by subplot/plot area (all sites combined). Vertical bars represent standard errors.

esting added benefit, we are using the ratio of native to non-native species at the multiple spatial scales as one environmental indicator of ecosystem condition. This has potentially broad application in comparing various land use practices and successional patterns, and to investigate species-environment relationships. This nested design can be shrunk (proportionately) for smaller-scale studies (e.g. thin riparian zones, tundra vegetation, lichen surveys, etc.). It can be expanded for larger-scale habitats (such as widely scattered tree habitats), but longer tapes and better field surveying techniques might be needed.

We are, unfortunately, far from standardizing field techniques for assessing plant species diversity at landscape scales. Decisions must be made about the number and the placement of plots needed to describe the plant species diversity of large study areas and landscapes (Stohlgren 1994). The timing of sampling, and species' rareness, and the patterns of landscape features must also be considered. Determining the efficiency of sampling in vascular plant species richness projects will depend on species discovery/accumulation rates and rate of observed changes (Heltshel & Forrester 1983; Miller & Wiegert 1989). Trend analysis from monitoring a series of strategically-placed, long-term Modified-Whittaker study plots may be a valuable tool for quantifying and detecting trends in vascular plant species richness.

Species-level plant distribution data at landscape scales are expensive to collect. Most species are rare

and complete surveys of large areas are generally cost prohibitive (Stohlgren & Quinn 1992). Cost-efficient standardized sampling techniques for other components of biodiversity must also be developed (Stohlgren *et al.* 1994).

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Appendix . Study site locations and vegetation types:

Site Name	Location, State	Elevation	Vegetation	Comments
1. Button Rock Forest	Button Rock Preserve, CO	2134m	Pine/C3/C4	Southeast facing, Ponderosa savanna
2. Taft Hill Disturbed Area	Fort Collins City Limit, CO	1554m	C3 Weedy Species	Deep soil, C3 dominated
3. Taft Hill Disturbed Area	Fort Collins City Limit, CO	1554m	C3/C4 Weedy/Prairie Mix	Deep soil, C3 dominated
4. Taft Hill Disturbed Area	Fort Collins City Limit, CO	1554m	C3/C4 Weedy/Prairie Mix	Deep soil, C3 dominated
5. Pineridge Prairie	Pineridge Open Space, CO	1631m	C3/C4 Weedy Species	Prairie dog colony
6. Pineridge Prairie	Pineridge Open Space, CO	1631m	C3/C4 Weedy/Prairie Mix	Prairie dog colony
7. Pineridge Prairie	Pineridge Open Space, CO	1631m	C3/C4 Weedy/Prairie Mix	Prairie dog colony
8. Pineridge Ecotone	Pineridge Open Space, CO	1634m	Pine/C3/C4 Prairie Mix	Forest/Prairie border, east facing
9. Pineridge Ecotone	Pineridge Open Space, CO	1634m	Pine/C3/C4 Prairie Mix	Forest/Prairie border, east facing
10. Pineridge Ecotone	Pineridge Open Space, CO	1634m	Pine/C3/C4 Prairie Mix	Forest/Prairie border, east facing
11. Pineridge Forest	Pineridge Open Space, CO	1695m	Pine/C3/C4	Ponderosa, east facing
12. Pineridge Forest	Pineridge Open Space, CO	1695m	Pine/C3/C4	Ponderosa, east facing
13. Pineridge Forest	Pineridge Open Space, CO	1695m	Pine/C3/C4	Ponderosa, east facing
14. Red Valley Grass	Wind Cave National Park, SD	1316m	C3/C4 Prairie	Upland, rocky, C4 dominated
15. Fire Tower Prairie	Wind Cave National Park, SD	1390m	C3/C4 Prairie	Deep soil, C3 dominated, west facing
16. Fire Tower Ecotone	Wind Cave National Park, SD	1396m	Pine/C3/C4 Prairie Mix	Forest/Prairie border, west-facing
17. Fire Tower Forest	Wind Cave National Park, SD	1402m	Pine/C3/C4 Prairie Mix	Rocky, pine dominated, west facing
18. Archer Hill Bottom	Wind Cave National Park, SD	1122m	C3/C4 Prairie	Deep soil, C3 dominated
19. Orchard East Midslope	Wind Cave National Park, SD	1176m	C3/C4 Prairie	Midslope east facing
20. Highland Creek E.	Prairie Wind Cave National Park, SD	1322m	C3/C4 Prairie	Deep soil, C3 dominated, east facing
21. Highland Creek E. Ecotone	Wind Cave National Park, SD	1335m	Pine/C3/C4	Forest Prairie border, east facing
22. Highland Creek E. Forest	Wind Cave National Park, SD	1341m	Ponderosa Pine/C3/C4 Mix	Rocky, pine dominated, east facing
23. Boland Ridge N. Prairie	Wind Cave National Park, SD	1243m	C3/C4 Prairie Mix	C3 dominated, north facing
24. Boland Ridge N. Ecotone	Wind Cave National Park, SD	1255m	Pine/C3/C4 Prairie Mix	Forest Prairie border, north-facing
25. Boland Ridge N. Forest	Wind Cave National Park, SD	1274m	Ponderosa Pine/C3/C4 Mix	Rocky, pine dominated, north facing
26. Boland South Midslope	Wind Cave National Park, SD	1183m	C3/C4 Prairie Mix	South facing, rocky soil
27. Five Six S. Bottom	Wind Cave National Park, SD	1158m	C3/C4	Deep soils, C3 dominated
28. Five Six S. Midslope	Wind Cave National Park, SD	1170m	C3/C4	South-facing
29. Five Six S. Upper	Wind Cave National Park, SD	1182m	C3/C4	C4 dominated, rocky
30. Look Out Upper	Wind Cave National Park, SD	1311m	C3/C4	C4 dominated, rocky
31. Custer E. Prairie	Wind Cave National Park, SD	1384m	C3/C4	C3 dominated, deep soil
32. Custer E. Prairie Ecotone	Wind Cave National Park, SD	1396m	Pine C3/C4	Forest/Prairie, east facing