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Plot shape effects on plant species diversity measurements

Keeley, Jon E.[1,2*] & Fotheringham, C.J.[2]

[1]*U.S. Geological Survey, Western Ecological Research Center, Sequoia National Park, Three Rivers, CA 93271, USA;* [2]*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA; E-mail seajay@ucla.edu; *Corresponding author; E-mail jon_keeley@usgs.gov*

Abstract

Question: Do rectangular sample plots record more plant species than square plots as suggested by both empirical and theoretical studies?

Location: Grasslands, shrublands and forests in the Mediterranean-climate region of California, USA.

Methods: We compared three 0.1-ha sampling designs that differed in the shape and dispersion of 1-m^2 and 100-m^2 nested subplots. We duplicated an earlier study that compared the Whittaker sample design, which had square clustered subplots, with the modified Whittaker design, which had dispersed rectangular subplots. To sort out effects of dispersion from shape we used a third design that overlaid square subplots on the modified Whittaker design. Also, using data from published studies we extracted species richness values for 400-m^2 subplots that were either square or 1:4 rectangles partially overlaid on each other from desert scrub in high and low rainfall years, chaparral, sage scrub, oak savanna and coniferous forests with and without fire.

Results: We found that earlier empirical reports of more than 30% greater richness with rectangles were due to the confusion of shape effects with spatial effects, coupled with the use of cumulative number of species as the metric for comparison. Average species richness was not significantly different between square and 1:4 rectangular sample plots at either 1- or 100-m^2. Pairwise comparisons showed no significant difference between square and rectangular samples in all but one vegetation type, and that one exhibited significantly greater richness with squares. Our three intensive study sites appear to exhibit some level of self-similarity at the scale of 400 m^2, but, contrary to theoretical expectations, we could not detect plot shape effects on species richness at this scale.

Conclusions: At the 0.1-ha scale or lower there is no evidence that plot shape has predictable effects on number of species recorded from sample plots. We hypothesize that for the mediterranean-climate vegetation types studied here, the primary reason that 1:4 rectangles do not sample greater species richness than squares is because species turnover varies along complex environmental gradients that are both parallel and perpendicular to the long axis of rectangular plots. Reports in the literature of much greater species richness recorded for highly elongated rectangular strips than for squares of the same area are not likely to be fair comparisons because of the dramatically different periphery/area ratio, which includes a much greater proportion of species that are using both above and below-ground niche space outside the sample area.

Keywords: α-diversity; Chaparral; Coniferous forest; Desert scrub; Grassland; Sage scrub; Savanna; Self-similarity; Shrubland; Species richness.

Introduction

Answers to both theoretical and applied questions in ecology commonly require empirical data from field sampling. Such data are essential for comparative biology, but comparisons are often complicated by data obtained with different sample designs. The so-called 'Whittaker plot' design described by Shmida (1984) has been widely utilized as an appropriate standard for comparing community diversity, although often with modifications (Peet et al. 1998). Recognition that species richness varied with scale led Whittaker (1977; Whittaker et al. 1979) to propose a 20 m × 50 m (0.1 ha) plot that recorded different scales of diversity in nested subplots (method W, Fig. 1a). Stohlgren et al. (1995) suggested that there were deficiencies in the Whittaker plot method and proposed a modification (method S) (Fig. 1b). One of the important conclusions of Stohlgren et al.'s (1995) study was that rectangular samples with length to width ratio of 1:4 generated substantially greater species richness than square samples, regardless of scale within the tenth ha plot. Indeed, they suggested as much as a 30% or more increase in species richness from the use of rectangular plots in their design over the Whittaker design. However, Stohlgren et al.'s (1995) study varied spatial dispersion and plot shape simultaneously by comparing methods W and S (Fig. 1a, b), and they utilized cumulative species richness as their metric, all of which made it impossible to separate shape effects from spatial effects.

This conclusion about dramatic differences to be expected with squares and rectangles is important because if the conclusions drawn by Stohlgren et al. (1995) are true, it casts doubt on the validity of many other vegetation studies. A comparative study of square and rectangular plots, where plot dispersion is not a confounding effect, is needed in order to answer whether shape matters. This is of practical concern to resource managers who utilize plot sampling to accomplish multi-scale inventories.

The purpose of this investigation was to test the null hypothesis that square and rectangular plots provide equal estimates of species richness. We compared three

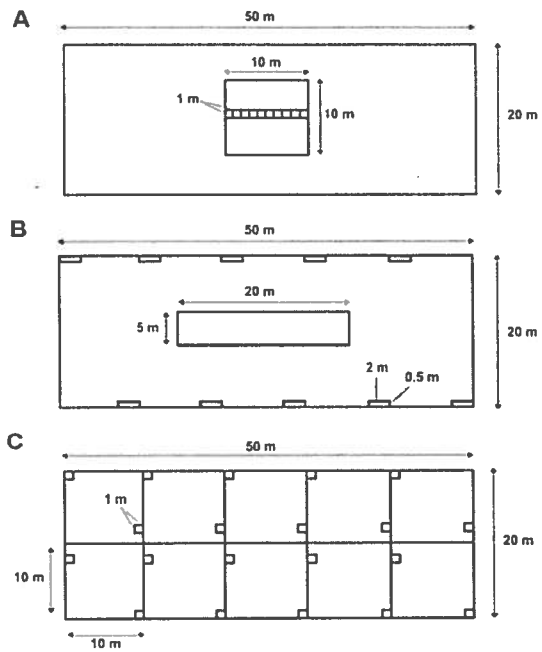

Fig. 1. The three 0.1-ha sampling methods contrasted in this study. Published methods vary in the sizes of nested subplots, but only 1-m^2 and 100-m^2 subplots used in the present study are shown. **A.** The Whittaker (W) design; **B.** Stohlgren's (S) modified Whittaker design, placement of subplots varies in different studies, here rectangular subplots are positioned so that there was a 50% overlap with the square subplots used in (K); **C.** the K (Keeley et al. 1995) design typically has 20 1-m^2 subplots, but (cf. Keeley et al. 2003) high density grasslands may necessitate sampling only the peripheral 10 subplots. See Table 1 for summary characteristics.

0.1-ha sample plot methods; the Whittaker (W) plot (Fig. 1a), Stohlgren's (S) plot (Fig. 1b) and one we have used (K; Fig. 1c) in several studies (Keeley et al. 1995, 2003; Schwilk et al 1997; Keeley 1998; Keeley & Fotheringham 2003). Here we contrast these three methods at scales of 1-m^2 and 100-m^2 in plots that differ in shape and dispersion within the 0.1-ha plot (Table 1). By overlaying these methods on the same tenth-ha plot we could compare rectangular (S) and square (K) 1-m^2 subplots that were partially overlaid on one another, reducing the spatial/shape interactions and evaluate the relative effect of plot shape vs dispersion pattern on species richness. In addition to direct comparisons at 1-m^2 and 100-m^2 scales, we made similar comparisons of square and rectangular designs at 400-m^2 using data from other studies (Keeley et al. 2003; Keeley & Fotheringham 2003). In order to evaluate Harte et al.'s (1999a, b) theoretical expectation that rectangles should record more species than squares (discussed below), we tested whether or not our communities fit the assumptions behind his models.

Plot shape background

Although studies of plot shape effects on species diversity are relatively recent, historically there have been a number of field studies that have examined the effect of plot shape on sampling variance in cover and density. Clapham (1932) found rectangles generated less variance in cover measurements than square plots, and this was interpreted as the most 'efficient' sampling design, or in other words it provided more precise measures of cover. Later Bormann (1953) drew similar conclusions, although he made no direct comparison of squares and rectangles with similar areas. In contrast, Myers & Chapman (1953) did make direct comparisons of rectangles and squares with the same area and concluded that plot shape had no consistent effect on sample variance.

Following Stohlgren et al.'s (1995) report of greater species richness from rectangular plots, Condit et al. (1996), reported narrow elongated strips also exhibited greater richness than squares of comparable total area. In contrast, Kunin (1997) found species richness at the 16-m^2 scale was not significantly different between squares and 1:4 rectangles or elongated strips, however, landscape level comparisons of 640 000 m^2 or more did show shape effects.

In support of empirical reports of plot shape effects are the theoretical conclusions of Harte et al. 1999a; Harte & Kinzig 1997). They found that if the proportion of species in common between patches remains constant regardless of scale (self-similarity), this will lead to a power model of species area relationships, and if there are no gradients in species richness, then rectangular plots will record substantially more species than square plots (Harte et al. 1999b; Harte 2000).

Table 1. Comparison of shape and dispersion patterns for 1-m^2 and 100-m^2 subplots nested in the 20m × 50m 0.1-ha plots (see Fig. 1 for spatial configuration).

	1-m^2			100-m^2	
	Shape	Dispersion	*n*	Shape	*n*
Whittaker (W)	Square	Clumped	10	Square	1
Stohlgren (S)	Rectangle	Dispersed	10	Rectangle	1
Keeley (K)	Square	Dispersed	20 (10)*	Square	10

* In communities with dense herbaceous vegetation, such as grasslands, sample size is reduced to the ten 1-m^{2}subplots on the periphery (e.g., Keeley et al. 2003).

Study sites and methods

We investigated the effect of plot shape in three vegetation types, including five ungrazed *Quercus douglasii* (blue oak) savanna sites, five grazed grassland sites, and five post-fire forest/chaparral ecotone sites. Sampling was done in the foothills of the southern Sierra Nevada Mountain Range in California, USA. Savanna sites were all in Sequoia National Park from 600 - 1000 m, cattle-grazed grasslands on adjacent Bureau of Land Management lands 400 - 500 m, and forest ecotone sites in the adjacent Sequoia National Forest 1150 - 1300 m. These communities were included to test the effect of plot shape in a variety of vegetation types, but not to contrast the effect between communities.

At each of the 15 sites, a comparison of W, S and K sampling methods (Fig. 1a-c) were conducted within the same 20 m × 50 m plot (i.e. Fig 1a was overlaid on 1b, and both were overlaid on 1c). Plots were placed in stands of seemingly homogeneous vegetation, which was the only criterion for plot placement used by Shmida (1984). We define homogeneous to be similar stature and mix of cover and bare ground. Stohlgren et al. (1995) did not specify how plots were placed, but later (Stohlgren et al. 1998) indicated they were "placed with the long axis [of the 20 m × 50 m plot] along the environmental gradient." They did not specify how one would determine this gradient, but it appears they did not consider this to be an important factor in their sampling since their 1-m^2 rectangular subplots were laid down both parallel and perpendicular to this gradient (Stohlgren et al. 1995 placed six along the long axes and four along the short axes, not shown in our modification illustrated in Fig. 1b). The semi-arid landscapes we studied do exhibit broad elevational gradients in species turnover, however, at the community scale such elevational patterns are not evident. Observations suggest that on these slopes an important determinant of species turnover is related to differences in drainage patterns. Since water drains parallel to the slope incline, we might expect, at the tenth-ha scale that the greatest variation in drainage patterns would be perpendicular to the slope. However, we could not, *a priori*, detect any consistent gradients, and thus we decided plots should be placed with the same orientation at all sites, and chose placement of the long axis along the elevational contour.

Within the 20 m × 50 m plot were nested 100-m^2 subplots and within these subplots were nested 1-m^2 subplots (Fig. 1). We modified W and S by excluding the 10-m^2 sample scale. In the case of the S design the precise placement of the 1-m^2 rectangular (0.5 m × 2 m) subplots has varied in different papers (cf. Stohlgren et al. 1995, 1998; Kalkhan & Stohlgren 2000). We have shifted slightly the placement of these subplots in method S (Fig. 1b) so that there was a 50% overlap with each of the square 1-m^2 subplots from method K (Fig. 1c). In prior studies using the K method, 20 1-m^2 subplots were always sampled in chaparral, desert scrub and coniferous forests (Fig. 1c), but in oak savannas, with higher density and cover of herbaceous vegetation, only the ten on the periphery were sampled (e.g. Keeley et al. 2003). In the present study ten were sampled in each oak savanna and grassland site and 20 in each of the post-fire forest ecotone sites. Within the 1-m^2 subplots all species were recorded and in the 100-m^2 subplots additional species were recorded.

Species richness was compared across all three sampling designs (Fig. 1) with a one-way fixed effects ANOVA (SYSTAT 10.0, www.systat.com). Since our interest was in shape effects and not community effects we did not use a nested design. A pooled *t*-test was used to test for significant effects of shape and dispersion, the former testing for significantly greater richness in rectangles with a 1-tailed *t*-test, the latter testing for no difference due to dispersion with a 2-tailed *t*-test. To test for effects of shape alone we used 1-m^2 paired square (K) and partially overlapping (S) rectangles (Fig. 1b, c) and tested for differences with a 1-tailed paired *t*-test. The Pearson χ^2 test statistic was used to compare whether there were more pairs at a site in which rectangles had more species than squares vs pairs where rectangles had fewer species than squares. For parametric statistics we tested for homoscedasticity with an *F*-test, and although we did not test for normality of error terms, the raw data were not highly skewed, which is generally considered sufficient in light of the robustness of ANOVA to assumptions of normality.

In order to extend this comparison to a larger spatial scale, and more communities, we used published data utilizing method K (Keeley et al. 2003; Keeley & Fotheringham 2003). This involved comparing 400-m^2 square subplots and partially overlapping 1:4 rectangular subplots. To do this the top two and bottom two 100-m^2 subplots at the left end of the plot (e.g. Fig. 1c) comprised the square 400-m^2 subplot. The rectangular 400-m^2 plot was made by combining the four contiguous 100-m^2 subplots along the top, beginning at the left, thus a rectangular subplot overlapped 50% of the square subplot. Data were available for 236 comparisons distributed between desert scrub in a high rainfall year and low rainfall year, coastal and interior sage scrub and chaparral, blue oak savanna, and unburned and burned coniferous forests in California. Pairwise *t*-tests were used to evaluate the differences between species richness recorded from squares vs rectangles within each vegetation type.

Self-similarity was evaluated by combining 100 m^2 subplots from our initial comparison study of *Quercus*

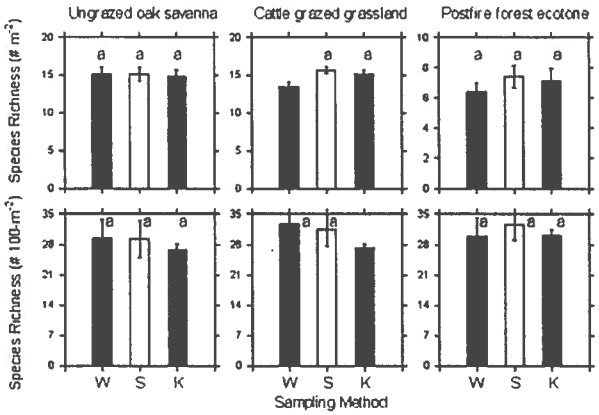

Fig. 2. Comparison of methods W, S and K for species richness in 1-m^2 and 100-m^2 subplots recorded with square (filled bars) and rectangular (open bars) samples. Within a panel, bars with the same letter are not statistically different at $P < 0.05$. Includes only species rooted in the plots.

douglasii (blue oak) savanna, grassland, and chaparral-forest ecotone (Fig. 1c) to generate data for plots of 200, 400 and 800 m^2, and for calculating the proportion of species in common between two halves of these plots. This is defined as statistical community-level self-similarity (Green et al. 2003). Species area curves were calculated with least squares regression on the nested subplots using a power model and an exponential model. Lack of independence is a potential problem with statistics calculated from regression analysis of nested designs, but previous comparison of this nested design with an unnested design in these arid land communities has failed to detect any substantial difference in the standard error of estimate (Keeley & Fotheringham 2003).

Results

Comparing the W, S and K sampling methods there was no statistically significant difference for two of the three communities (Fig. 2). The significant differences recorded in the third community (grasslands) did not suggest plot shape effects were important, because at the 1-m^2 scale, squares and rectangles on the periphery (S and K) were similar to each other, but significantly different from squares in the centre of the site (W). At the larger scale the square and rectangular plots in the centre of the site (W and S) were similar to each other, but significantly different from the squares distributed around the periphery (K).

Table 2 separates shape effects from spatial dispersion effects by comparing all 1-m^2 square subplots (regardless of dispersion pattern, W and K) with rectangular subplots (S), and then all dispersed subplots (regardless of shape, S and K) with clustered subplots (W). Plot shape had no significant effect on species richness, at both 1-m^2 and 100-m^2 scales, in any of the vegetation types. Spatial dispersion did have a significant effect at both scales in one of the vegetation types, being greater in dispersed plots.

Another means of separating out shape effects from spatial dispersion effects is to focus on just those plots that differ in shape, but not in patterns of dispersion, namely the 1-m^2 squares from K and partially overlapping rectangles from S (Fig. 1b, c). Since we are contrasting pairwise subplots of different shape, and are not contrasting different communities, it is appropriate to combine data from all sites of a particular community type. This comparison showed there was no significant difference in species richness between rectangles and squares (Table 3). When pairs were tallied, it turned out that in two of the communities there were actually more squares that exceeded their paired rectangles than rectangles that exceeded squares, however, this was not statistically significant (Table 3).

In order to expand the spatial scale of comparisons and vegetation types, we compared 400-m^2 square and overlapping 1:4 rectangular plots from desert, chaparral, sage scrub, savannas, and forests (Table 4). In no case did rectangular plots record greater species richness than square plots. Two communities were significant or

Table 2. Comparison of the effect of plot shape, i.e. rectangular (S) vs. square (W and K), and of the effect of dispersion, i.e. clumped (W) vs. dispersed (S and K), on species richness at 1 m^2 and 100 m^2 with the three sampling techniques illustrated in Fig. 1 and sample sizes noted in Table 1.

	Ungrazed savanna		Grazed grassland		Post-fire forest ecotone	
Factor	*t*-value	*P*	*t*-value	*P*	*t*-value	*P*
Species richness (# 1-m^{-2})						
Shape	0.329	0.743	1.410	0.279	0.347	0.729
Dispersion	0.247	0.806	2.450	0.015	0.801	0.424
Species richness (# 100-m^{-2})						
Shape	0.534	0.595	1.303	0.198	0.522	0.604
Dispersion	0.074	0.941	−1.867	0.046	−0.573	0.569

Table 3. Comparison of species richness, without confounding effects of differences in dispersion, using the squares from method K and paired with partially overlapping rectangles using method S (Fig. 1b, c) for 1-m^2 subplots.

Vegetation	Species richness (# 1-m^{-2})			Number of pairs where rectangles		
	Rectangles	Squares	*P*	> squares	< squares	*P*
Ungrazed savanna	16.1	15.8	0.168	21	15	0.265
Grazed grassland	15.9	15.8	0.451	16	19	0.353
Postfire forest ecotone	8.6	8.2	0.218	13	24	0.125

close to statistical significance, but both were ones where squares had greater richness than rectangles. Thus, rectangles not only did not sample greater species richness but there was not even a trend towards greater richness in rectangles. Across all 236 sites, fewer than half had greater species richness for rectangular plots (Table 4).

The three communities used in the initial comparison were also utilized in our examination of the assumptions behind Harte's theoretical models that predict rectangles will record greater species richness than squares. These communities appear to exhibit self-similarity as the proportion of species in common for half of a patch remained roughly the same at scales of 200, 400, and 800 m^2 (Table 5). Specifically, in savannas the proportion ranged from 0.806 - 0.831, in grasslands 0.832 - 0.862, and in forests from 0.763 - 0.795 (Table 5). Least squares regression of the power model (log species vs log area) gave higher R^2 values than the exponential model (species vs log area) for oak savanna, grassland and forest (Table 5), and the power model residuals demonstrated less heteroscedasticity, indicating a somewhat better fit to the power model. Despite being self-similar, and approximating a power model species area relationship, square and rectangular plots did not differ in species richness (Table 5).

Discussion

For many different Californian plant communities, rectangles with a 1:4 length to width ratio, across scales from 1 to 400 m^2, do not record species richness differently from square samples. In many instances the trend was towards more species in squares, and thus it is unlikely that larger sample sizes would show rectangles are superior to squares. Considering the range of vegetation types included here (grassland, savanna, coniferous forest, chaparral, coastal sage scrub, and desert scrub), there seems little reason to assume this conclusion is an artifact of a particular community. Indeed, Kunin (1997) studied very different temperate plant communities, and at the community level scales we are dealing with, he too found that rectangles did not surpass squares in recording species richness.

These findings contradict the contention by Stohlgren et al. (1995) that rectangular plots used in S (Fig. 1b) are much more efficient than square plots, which they claimed recorded greater than 30% more species. We contend that their conclusion is clouded by the fact that they varied both shape and spatial dispersion simultaneously by comparing W and S methods (see Table 1). The present study allows one to sort out shape and spatial effects, and shape has no discernable effect at these scales (Table 3).

Table 4. Comparison of species richness in 400-m^2 squares (20 m × 20 m) vs partially overlapping rectangles (10 m × 40 m) from published data (Keeley et al. 2003; Keeley & Fotheringham 2003).

	Species richness (# 400-m^{-2})				Number of pairs where rectangles	
	Squares	Rectangles				
Vegetation	$\bar{X}$ ± SD	$\bar{X}$ ± SD	(*n*)	*P*	> squares	≤ squares
Desert scrub in high ppt yr	42.1 ± 15.2	42.7 ± 14.2	(15)	0.563	8	7
Desert scrub in low ppt yr	8.5 ± 3.2	8.9 ± 3.4	(15)	0.433	7	8
Coastal sage scrub	32.2 ± 6.6	32.0 ± 6.9	(21)	0.851	9	12
Interior sage scrub	40.4 ± 8.3	38.6 ± 8.4	(27)	0.048	9	18
Coastal chaparral	34.4 ± 6.3	31.8 ± 5.7	(14)	0.075	3	11
Interior chaparral	33.4 ± 13.8	32.7 ± 12.0	(26)	0.507	11	15
Blue oak savanna	40.7 ± 7.9	40.6 ± 9.0	(15)	0.898	7	8
Mature conifer forest	13.5 ± 4.6	14.2 ± 4.6	(19)	0.366	9	10
Burned conifer forest	21.0 ± 1.1	21.8 ± 1.3	(84)	0.179	43	41
				Total	106	130

Table 5. Using data from this study with technique K for estimating whether or not these data fit Harte's assumptions of self-similarity and power model species area relationship (SAR) R^2 for power and exponential models.

	Proportion of species in common between						SAR Model		Species richness (400 m²)			
	100 & 200 m²	200 & 400 m²	400 & 800 m²				Power	Exp.	Squares	Rectangles		
	$\bar{X} \pm$ SE	$\bar{X} \pm$ SE	$\bar{X} \pm$ SE	(n)	F	P	R^2	R^2	$\bar{X} \pm$ SE	$\bar{X} \pm$ SE	t	P
Savanna	0.806 ± 0.036	0.829 ± 0.020	0.831 ± 0.029	(5)	0.218	0.808	0.621	0.518	39.8 ± 5.0	39.2 ± 5.4	1.000	0.374
Grassland	0.848 ± 0.038	0.832 ± 0.041	0.862 ± 0.018	(5)	0.198	0.832	0.887	0.736	44.2 ± 3.0	41.4 ± 0.8	0.884	0.427
Forest	0.795 ± 0.035	0.763 ± 0.023	0.775 ± 0.049	(5)	0.183	0.835	0.924	0.709	55.8 ± 5.4	57.0 ± 6.1	0.242	0.821

A major part of the explanation for substantially greater richness reported with Stohlgren's modified Whittaker technique is the metric they used for comparing rectangles and squares. They added up the cumulative number of species in ten 1-m² rectangles dispersed over a 1000 m² area, and compared this number with the cumulative number of species in ten 1-m² squares clumped together over a total area of only 10 m² (Stohlgren et al. 1995). It has long been known that this metric of cumulative number of species is difficult to interpret for spatially disjunct samples (Bormann 1953), and even more so when comparisons are being made between very different sized areas (Lande et al. 2000). In terms of fractal geometry, the ten subplots in W (Fig. 1a) comprised a large window of contiguous grains separated by a short lag distance, whereas the ten subplots in S (Fig. 1b) comprised smaller windows with much greater lag distance between grains (Milne 1991). As lag distance increases, cumulative number of species is expected to increase because one is increasing the range of environments being sampled.

The present study avoided these problems by using a different metric, namely the average number of species per m² that can be calculated from the ten 1-m² plots. This measure of species richness is more widely used because it is a measure of the number of species that can coexist in 1 m², whereas cumulative number of species spread over 0.1 ha has a much less precise definition.

However, not all reports of rectangles recording more species than squares can be explained by either spatial effects or metrics of comparison. Condit et al. (1996), for example, reported tropical rainforest species richness in 2 m × 200 m strips exceeded the richness in 20 m × 20 m squares. They attributed this effect to the rectangular strips crossing more environmental gradients, but Barbour et al. (1999) suggest that sampling accuracy declines as a plot lengthens because of the 'edge effect', which is a sampling artifact due to having to make decisions about including individuals on the periphery. In Condit et al.'s (1996) study this error could be rather large because the periphery was over five times greater for the rectangular strips than for squares. There is an additional, and more important error associated with the use of elongated strips, particularly when the width of the strip is markedly smaller than the scale of the vegetation being sampled. When sampling tropi-

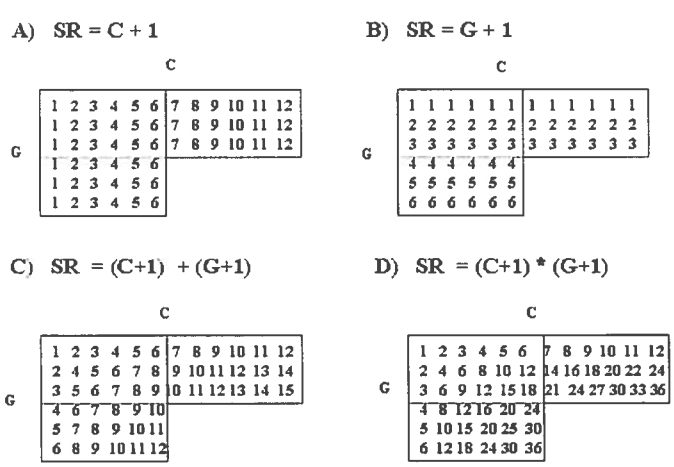

Fig. 3. Partially overlapping square and rectangular plots illustrating different patterns of change along environmental gradients C and G, where numerals indicate cumulative number of species at a particular coordinate. At the origin in the upper left corner C = G = 0, and these axes are manipulated by algorithms that yield the cumulative number of species as the plot size is expanded from the origin in the C and D directions. If one imagines species richness increasing from the origin in the upper left corner, the total species richness recorded in the plot will be evident in the lower right corner of both rectangles and squares. In (**A**) only one gradient affecting species richness parallel to the long axis of the rectangle; (**B**) one gradient perpendicular to long axis of the rectangle; (**C**) multiple gradients species increase independently in an additive fashion along both gradients; (**D**) species interact multiplicatively along both gradients.

cal rainforests with 2 m wide strips it is likely that a high proportion of individuals are not wholly contained within the plot, thus exaggerating the actual area being sampled. Even for plants in which the stem is wholly contained within the plot, rooting area and canopy are likely to exceed the narrow dimension of the sampled strip. Thus, elongated strips potentially are sampling richness over niche space greatly exceeding the presumed sample area. This effect would be substantially smaller in squares due to the smaller periphery:area ratio.

Our results also appear to contradict theoretical predictions. Harte et al. (1999a, b) used principles of fractal geometry to argue that when plant communities exhibit self-similarity, rectangular plots will record a greater number of species than square plots. Our three intensively studied communities appear to exhibit self-similarity and no plot shape effect on species richness at 400-m^2 (Table 5). One possible reason for this discordance with theory is that self-similar communities are predicted to fit a power model for the species area relationship, where fit is defined as an $R^2 > 0.98$ (Harte et al. 1999a; Green et al. 2003). This restrictive definition would seem to eliminate a power model fit for our communities (Table 5), and many plant and animal communities (e.g. Conner & McCoy 1979; Rosenzweig 1995; Keeley & Fotheringham 2003).

Another reason why theoretical predictions of plot shape effects may not be supported by our empirical results at several different scales has to do with gradients in species distribution. Harte et al.'s (1999a, b) theory considers only environments where " there are no large-scale gradients favouring significantly more species" in one direction over another. We suspect this may not be true on many landscapes, and other studies have demonstrated gradients in species turnover in various directions (e.g. Whittaker 1967; Gauch 1973; Peet 1981; Cody 1986; Klausmeier 1999).

We hypothesize that the structure of species gradients is key to understanding the effect of plot shape and have outlined several possible gradients (Fig. 3). If there is only one relevant environmental gradient, and the long axis of rectangular plots follow that gradient, then species richness will exceed richness recorded from square plots (Fig. 3a). But, rectangles that double the length of the long axis, while maintaining a constant area, loose 50% of the width of the perpendicular axis. If the environmental gradient influencing species turnover is perpendicular to the long axis of the rectangle, rectangular plots will in fact result in less diversity (Fig. 3b). In reality, environmental gradients exist in more than a single dimension, and while rectangles potentially gain environmental variability along one gradient, they loose variability along the gradient perpendicular to the long axis. Thus, the influence of plot shape will be a function of how the community is structured. If species turnover along each axis is additive (Fig. 3c), then the gain along the long axis will be greater than the loss along the short axis. However, if there is an interaction between the rate of change along each axis, this multiplicative model (Fig. 3d) would, predict equal richness for squares and rectangles.

Our empirical results failed to detect consistent differences between squares and rectangles in number of species recorded at scales of 1, 100 and 400 m^2, and we suggest either these environments are structured as in Fig. 3d, or sites vary, with some sites having the greatest species turnover along the elevational contour (Fig. 3a) and other sites perpendicular to the contour (Fig. 3b).

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