



Species-area curves and estimates of total species richness in an old-field chronosequence

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Received 27 May 1997; accepted in revised form 2 March 1998

Key words: Cedar Creek, Diversity, Succession

Abstract

Average species-area curves were generated for vascular plants in 20 old-fields that were sampled in 1983, 1989, and 1994. These curves were fit with a saturating function to estimate total species richness for each old-field. Additional estimates of total species richness were generated by fitting the same saturating function to subsets of the species area curves and with a first-order jackknife procedure. Estimates of total species richness were strongly correlated with observed species richness. There was limited evidence suggesting that greater sampling was necessary to identify the same proportion of species in older, more species-rich old-fields.

Introduction

Ecologists have long recognized that there is a relationship between species diversity and area. Species-area curves were used to characterize plant communities early in the 20th century, and early plant ecologists attempted to characterize communities or identify the minimum area of a plant community based on the shape of the relationship between diversity and area (Arrhenius 1921, Gleason 1922, 1925, Goodall 1952; Hopkins 1957). Although some of the initial attempts to characterize plant communities by the shape of their species-area curves were not successful, the observation that more species are found in larger areas remains one of the most consistently reported patterns in ecology.

One application of species-area curves has been to estimate the number of species in an area when exhaustive sampling is not possible. Both Baltanas (1992) and Palmer (1990, 1991) compared various methods of estimating total species richness, including methods based on species-area relationships. Each author concluded that various methods could be used when comparing relatively similar areas, but they suggested that there may be some uncertainty when applying those methods to dissimilar communities (e.g.,

tropical vs mid-latitude) or to larger spatial scales than those at which their tests were performed.

Estimation of total species richness by extrapolation may be most appropriate when comparing relative diversity of sample areas along an experimental or natural gradient (Palmer 1990). Under these conditions, the bias that has been demonstrated in most estimators may not be critical as long as it is consistent across the gradient. However, if there are consistent trends in characteristics of the sample areas that influence the behavior of an estimator, the use of the resulting estimates of total species richness may not be appropriate. If species richness or the pattern of relative species abundances change along a successional gradient, use of a single estimator of species richness may give a misleading picture of successional changes if the behavior of that estimator is not consistent across the range of values that is present.

The need to estimate total species richness is likely to become more common in the face of increased concerns about rates of extinction and the conservation of biological resources. Constraints on the resources that are available to sample communities will make it even more important to define sampling regimes that are likely to produce the most accurate estimates of diversity.

In this paper I use data from a chronosequence of old-fields to identify relationships between vascular plant diversity and sampling effort (species-area relationships), to test for differences in those relationships as a function of field age, and to determine the sampling effort that would be necessary to identify various percentages of plant species present in old-fields of different ages. I also compare estimates of total species richness that are based on the species-area relationship and on a first-order jackknife procedure.

Methods

The Cedar Creek Natural History Area (Cedar Creek) is located about 50 km north of Minneapolis, MN, USA, on a glacial outwash sandplain. Soils are very sandy and are low in organic matter (Grigal et al. 1974). Prior to settlement by farmers of European descent, vegetation at Cedar Creek was dominated by wetlands in low lying areas, by fire-maintained oak savanna, and by closed canopy forest in upland areas that were protected from fire by wetlands. Savanna vegetation consisted of scattered burr oak (*Quercus macrocarpa*) trees in a grassland matrix dominated by herbaceous species characteristic of tallgrass prairie. Areas in and around Cedar Creek were plowed and cultivated late in the 1800's, and many of these cultivated areas were abandoned from agriculture starting in the 1920's. Following abandonment from cultivation, vegetation in those old-fields has increased in total cover and in the abundance of species characteristic of tallgrass prairie (Inouye et al. 1987).

In 1983 vegetation was sampled in 19 old-fields that ranged in age from 1 to 56 years since abandonment from cultivation (Inouye et al. 1987). Four parallel transects, 40 m long and 25 m apart, were established in each old-field. Along each transect 25 1×0.5 m quadrats were located at 1 m intervals, with quadrats offset from the transect by 1 m and with their long axis perpendicular to the transect. Vegetation was sampled in each quadrat by visually estimating percent cover for each vascular plant species, for nonvascular plants, and for litter. Cover for each plot totaled 100%. The same quadrats were resampled in 1989 and in 1994. One additional field, #28, abandoned from agriculture in 1992, was first sampled in 1994.

Relationships between cumulative species richness (SR) and number of quadrats sampled (species-area curves) were identified for each old-field using data for each sample year. Because the precise shape of

these relationships can vary depending on the order in which plots are sampled, average values were calculated for randomly drawn sets of quadrats. Average SR on all 100 quadrats was used for a sample size of one quadrat. For sample size of 2–80 quadrats, 400 different randomly drawn sets of quadrats were identified for each sample size. For sample sizes of 81–98 quadrats, 300 different randomly drawn sets of quadrats were identified for each sample size. For a sample size of 99 quadrats, all 100 possible sets of 99 quadrats were identified, and total SR was used for the full sample of 100 quadrats. Average, minimum, and maximum cumulative SR were then calculated for each sample size of 1–99 quadrats.

To determine how sensitive average cumulative SR was to the number of sets, and in particular to see if 300 sets was an adequate sample size, average, minimum, and maximum cumulative SR were calculated for 1–2600 different sets of 2, 4, 6, 8, and 10 quadrats. These analyses were performed only with the 1994 data.

Estimated values for SR in each old-field were calculated in three ways. The first estimate (ESTSR1) was based solely on the average values of cumulative SR calculated for each sample size of quadrats. Average values of cumulative SR for sets of 1–100 quadrats were fit with the function $Y = 1/(A + (B/X))$. This function asymptotically approaches a maximum value of Y as X increases, reflecting the assumption that a maximum value of SR will be obtained as more quadrats are sampled within an old-field. This function was fit to data for each sample year, providing three estimates of total SR for each old-field (except for #28, sampled only in 1994). A second saturating function ($Y = (A \times X)/(B + X)$, the Michaelis-Menten equation) was also fit to the species-area data for each old-field and each sample year.

A second estimate of SR for each old-field (ESTSR2), made only using the 1994 data, was made by fitting the same saturating function to subsets of the average cumulative SR data to determine a predicted value of SR for 5, 10, 15, ... 100 quadrats. Based on that function, a predicted value of total SR was identified for each of these subsets. These predicted values were then in turn plotted against the number of quadrats used to calculate them, and the same saturating function was fit to these estimates of total SR to predict how estimated SR would have increased with additional sampling effort.

The third estimate of SR (JACK1), also made only using the 1994 data, was based on a first-order jack-

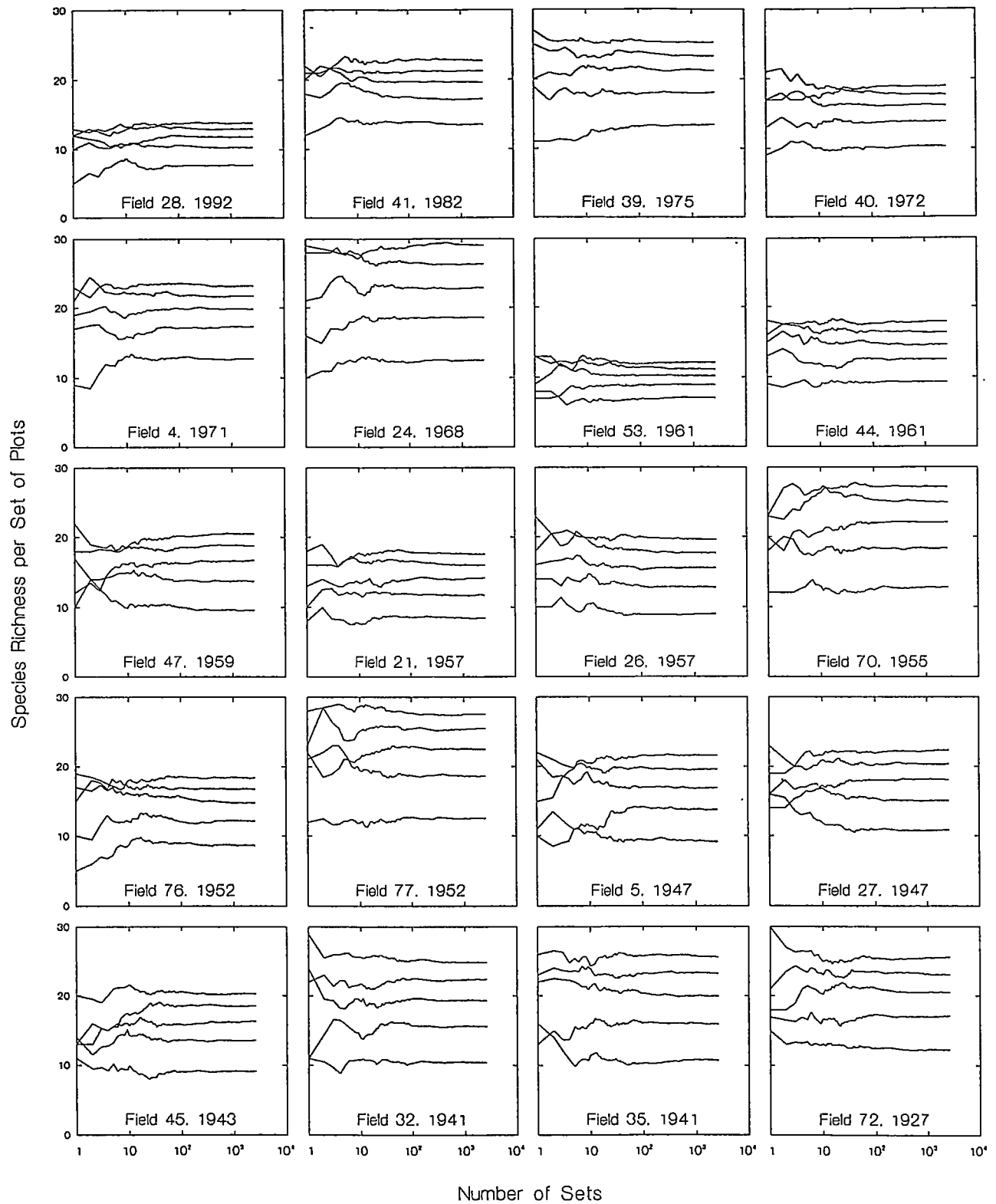


Figure 1. Species richness per set of quadrats as a function of the number of sets sampled for each of 20 old-fields. The five lines in each graph, from lowest to highest, represent 1994 data for sample sizes of 2, 4, 6, 8, and 10 quadrats. Numbers of sets ranged from 1 to 2800, and are plotted on a \log_{10} axis to illustrate the variation in average SR for small numbers of sets (<100). Old-fields are sorted in increasing age from left to right and from top to bottom. Some of the lines cross where the number of sets is very low because data for each sample size were generated independently by randomly drawing quadrats from the pool of 100 quadrats sampled in each old-field.

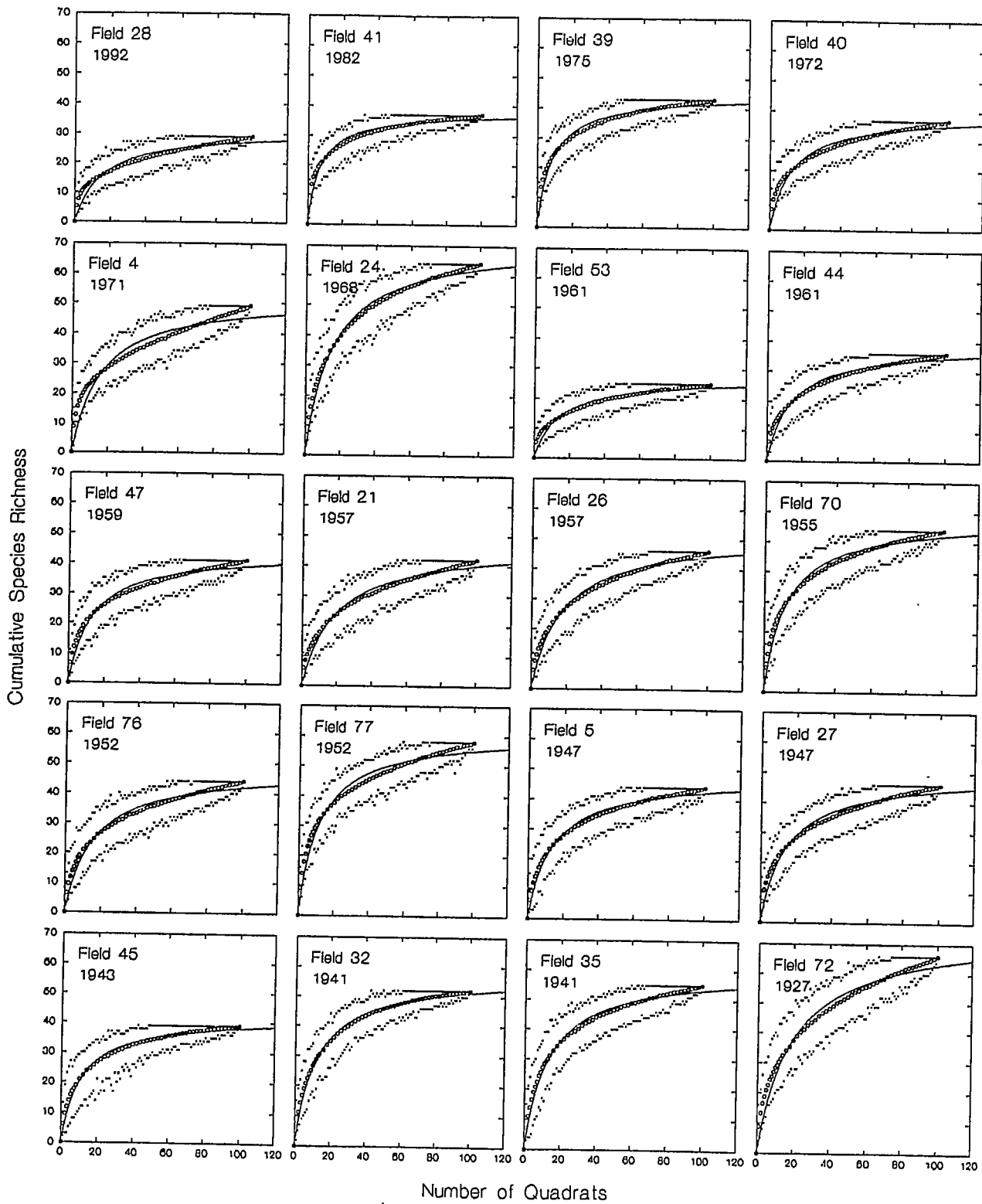


Figure 2. Average cumulative species richness (open circles) as a function of the number of quadrats sampled for each of 20 old-fields. The upper and lower sets of points represent maximum and minimum SR per set, and the solid line is the function $Y = 1/(A + 1/X)$ fit to the average values. Old-fields are sorted in increasing age from left to right and from top to bottom. For clarity, only every other value of average cumulative SR is plotted for numbers of quadrats greater than 10.

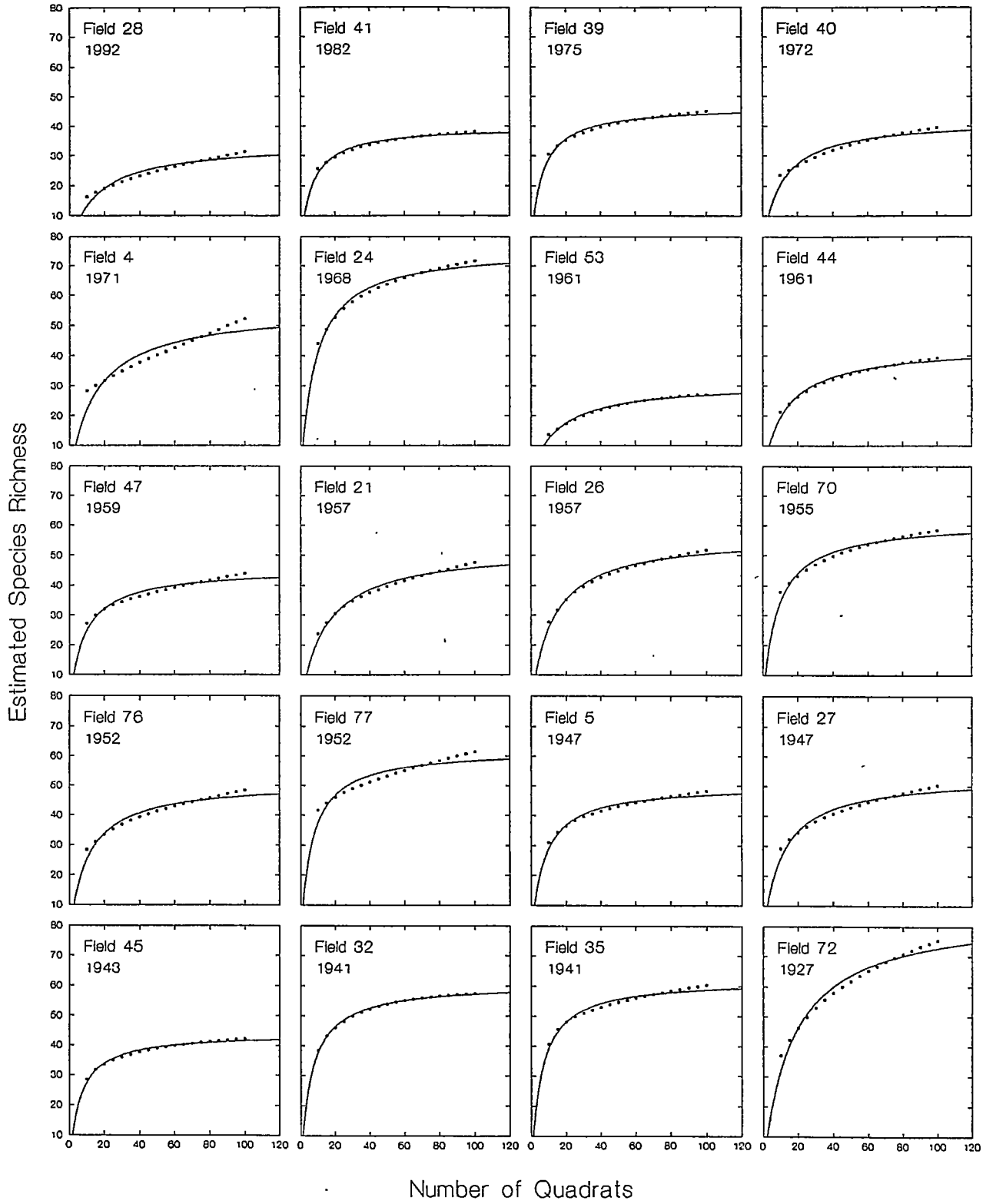


Figure 3. Estimated species richness (SR) as a function of the number of quadrats sampled for each of 20 old-fields. Estimates of SR were calculated by fitting the function $Y = 1/(A + 1/X)$ to values for average cumulative SR (plotted in Figure 2), using different numbers of quadrats.

knife procedure (Heltshe & Forrester, 1983). This procedure uses the total number of sample quadrats (100) and the number of species recorded on only one quadrat to estimate the number of species that were present but not sampled in any quadrat.

Necessary sampling effort was defined as the number of quadrats necessary to identify a particular percentage of species estimated to be present in an old-field. This was estimated using the average cumulative SR curves and the first estimate of total SR (ESTSR1).

Results

Average cumulative SR was sensitive to the number of randomly drawn sets of quadrats when the number of sets was less than 60–100, however it showed very little variation (<1%) for numbers of sets that ranged from 100 to 2600 (Figure 1). For large numbers of sets (i.e. >100), average SR for larger sets (e.g. 8 or 10 quadrats) was greater than for smaller sets (e.g., 2 or 4 quadrats). This difference among the 5 lines can be clearly seen at the right side of each graph in Figure 1. For small numbers of sets (i.e., <10) this was not always the case (e.g., Fields 41, 47, 76), illustrating the effect that sampling order can have on species area curves. The rate at which average SR increased with increasing set size declined, illustrated by the fact that the top lines in each graph are closer together than the bottom lines. This is consistent with the decreasing slope of species-area curves in Figure 2. Although average cumulative SR was relatively insensitive to sample sizes greater than 100, minimum and maximum values of cumulative SR continued to increase for some old-fields as the number of sets approached 2800. This reflects the very large number of possible sets of quadrats, and the low probability of drawing the exact set of quadrats with the minimum or maximum SR out of a pool of 100 quadrats.

Species-area curves for each old-field in 1994 are plotted in Figure 2; results for 1983 and 1989 were similar in shape but total observed SR varied somewhat among years (Table 1). Values for average cumulative SR gave significant fits to the saturating function, with most r^2 values greater than 0.95 and none less than 0.91. With one exception (field 41 in 1983), ESTSR1 was greater than observed SR. ESTSR1 was highly correlated with observed SR in each of the three years (all r^2 values >0.94, all $p < 0.001$). These values of ESTSR1 suggest that, on average, 92–94% of the species present in each old-field were recorded in

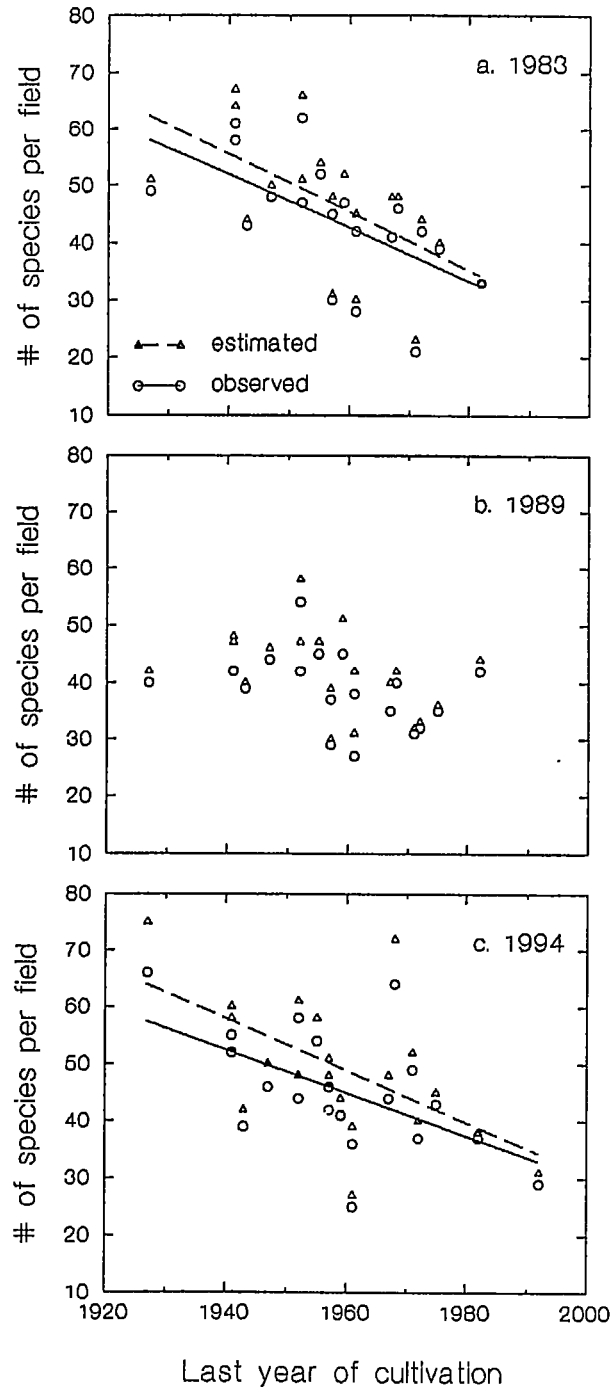


Figure 4. Observed (on 100 quadrats) and estimated field species richness (ESTSR1) plotted against last year of cultivation for 1983, 1989, and 1994. Estimated SR was calculated from the equation $SR = 1/(A + B/NPLOTS)$, where $1/A =$ estimated SR.

Table 1. Old-field number, last year of cultivation, observed species richness (Obs), and estimated species richness for 20 old-fields. ESTSR1 was calculated by fitting the equation $SR = 1/(A + 1/NPLOTS)$ to average values of cumulative SR for 1 through 100 quadrats (SR = estimated SR, NPLOTS = number of quadrats sampled). For 1994, ESTSR2 was calculated using the same equation fit to values of estimated SR based on varying numbers of sample quadrats. JACK1 was calculated using a first-order jackknife procedure.

Field No.	Last cultivated	1983		1989		1994			
		Obs	ESTSR1	Obs	ESTSR1	Obs	ESTSR1	ESTSR2	JACK1
4	1971	21	23	31	32	49	52	56	69
5	1967	41	48	35	40	44	48	50	54
21	1957	30	31	29	30	42	48	52	56
24	1968	46	48	40	42	64	72	76	77
26	1957	45	48	37	39	46	51	57	59
27	1947	48	50	44	46	46	50	53	57
28	1992	-	-	-	-	29	31	34	39
32	1941	61	67	42	47	52	58	61	58
35	1941	58	64	42	48	55	60	62	67
39	1975	39	40	35	36	43	45	47	49
40	1972	42	44	32	33	37	40	42	45
41	1982	33	33	42	44	37	38	40	42
44	1961	42	45	38	42	36	39	43	44
45	1943	43	44	39	40	39	42	44	44
47	1959	47	52	45	51	41	44	46	51
53	1961	28	30	27	31	25	27	31	31
70	1955	52	54	45	47	54	58	61	64
72	1927	49	51	40	42	66	75	85	87
76	1952	47	51	42	47	44	48	51	57
77	1952	62	66	54	58	58	61	62	72

at least one of the 100 quadrats. Fitting the Michaelis-Menten equation to the species-area data gave results that were very similar to those reported in Table 1.

Results of the second estimates of total SR (ESTSR2) are illustrated in Figure 3 and listed in Table 1. For many old-fields the estimates of total SR that were based on different numbers of quadrats showed a decreasing rate of increase with sample size. For these old-fields (e.g., fields 41, 45, 32), ESTSR2 was close to the ESTSR1 (Table 1). For some old-fields, however, the relationship between estimated total SR and sample size was close to linear, suggesting that a larger proportion of species present in those old-fields were not recorded in the 100 quadrats (e.g., fields 4, 77).

Results of the jackknife estimate were most similar to ESTSR2, and were, with one exception (#32), greater than ESTSR1. ESTSR2 and JACK1 were both highly correlated with observed SR (ESTSR2: $r^2 = 0.952$, $p < 0.001$; JACK1: $r^2 = 0.934$, $p < 0.001$).

Observed total SR was negatively correlated with last year of cultivation in 1983 and in 1994, but not

in 1989 (Figure 4). In 1994 the difference between observed SR and ESTSR1 was negatively correlated with last year of cultivation, indicating that a larger proportion of ESTSR1 was observed in more recently abandoned old-fields. This relationship is illustrated by the difference in slopes of the two lines in Figure 4c. There was no difference between the slopes of the two lines in Figure 4a, indicating that the difference between observed total SR and ESTSR1 was not correlated with last year of cultivation.

In 1994, ESTSR2 and JACK1 were both negatively correlated with last year of cultivation (ESTSR2: $r^2 = 0.350$, $p = 0.006$; JACK1: $r^2 = 0.265$, $p = 0.020$). The difference between ESTSR2 and observed SR was negatively correlated with last year of cultivation ($r^2 = 0.297$, $p = 0.013$), however the difference between JACK1 and observed SR was not significantly correlated with last year of cultivation ($r^2 = 0.084$, $p = 0.214$).

Figure 5 shows, for the 1994 data, the number of quadrats that would have to be sampled to observe

6 different percentages of the estimated total SR in each old-field. There was a significant relationship between the number of quadrats needed to identify 30% of estimated SR and last year of cultivation, and trends for the remaining percentages, while not statistically significant, were consistent with that relationship. These patterns suggest that a greater amount of sampling is necessary in older, more species-rich, old-fields to observe the same proportion of total SR. Similar analyses were performed using the observed total SR rather than estimated total SR. Those analyses revealed statistically significant negative relationships between number of quadrats and last year of cultivation for 30% ($r^2 = 0.276$, $p = 0.017$) and 40% ($r^2 = 0.280$, $p = 0.016$), and nonsignificant relationships for 50% ($r^2 = 0.128$, $p = 0.122$), 60% ($r^2 = 0.028$, $p = 0.479$), 70% ($r^2 = 0.020$, $p = 0.556$), and 80% ($r^2 = 0.006$, $p = 0.742$) of observed SR. In contrast to what was observed in the 1994 data, examination of the 1983 and 1989 data revealed no relationships between sampling effort necessary to observe various percentages of species and last year of cultivation.

Discussion

Species-area curves for 20 old-fields behaved much as expected, with cumulative SR increasing rapidly for small numbers of quadrats and more slowly as the number of quadrats approached 100. The saturating function that was fit to these curves explained a large proportion of the variance in cumulative SR, however there were consistent deviations between the function and the data. For all old-fields, and for each of the sample years, average cumulative SR increased more rapidly than the saturating function at small numbers of quadrats (<10), and exceeded values predicted by the saturating function when the number of quadrats was greater than 90. Fitting the Michaelis-Menten equation to the species-area data resulted in exactly the same pattern of deviations. Despite these differences, estimated values of total SR predicted by these curves (ESTSR1) were closely correlated with observed total SR, and predicted values exceeded observed values, on average, by less than 8%. This agreement between observed and estimated values of SR, and the shape of the species-area curves (Figure 1), suggest that most of the species present in each old-field were found in at least one of the 100 sample quadrats, and that the pattern between species richness and old-field age

reported by Inouye et al. (1987) was not strongly influenced by the intensity of sampling.

Differences among some old-fields, and deviations between the saturating function and average species-area curves, were more apparent when a second estimate of total SR was made by fitting the same saturating function to different subsets of the average species-area data (Figure 3). For all but two old-fields the saturating function explained more than 92% of the variance in estimated SR. For the remaining two old-fields the function explained less of the variance (#4: 88%; #77: 89%), and for these two old-fields the data were nearly linear with little decrease in slope at larger sample sizes. Despite those possible few exceptions, ESTSR2 was strongly correlated with observed SR and with ESTSR1.

With few exceptions, the first-order jackknife estimates were higher than the other estimates of SR. This is consistent with the results of Heltshe & Forrester (1983), who reported that for sample sizes of more than about 50 quadrats a first-degree jackknife gave estimates that were higher than either the observed or the actual SR. The old-fields for which the difference between observed SR and JACK1 was greatest (e.g., #4, #72, #77) are those that contained a relatively large number of species that were found in only one quadrat. Species-area curves in those old-fields showed the least sign of approaching an asymptote.

For most old-fields observed SR and ESTSR1 were lower in 1989 than in 1983, a pattern that is not consistent with the relationships plotted in Figures 4a and 4c. This discrepancy is most likely due to the severe drought that occurred in 1987 and 1988, and which resulted in significantly reduced vascular plant biomass and diversity on experimental plots that were monitored annually before, during, and after the drought (Tilman & El Haddi 1992).

As noted by Goodall (1952), and more recently by Rosenzweig (1995), species-area curves have been generated using at least three different sampling regimes. Aggregating plots of the same size to create larger sample units, the approach used here, is likely to result in a species-area curve that is initially higher than one generated by adding larger and larger areas to an initial quadrat of the smallest size. This is particularly true where there is greater patchiness in the spatial distribution of species because it will take longer to accumulate species with a sample area that is enlarged around an initial sample. Both of these methods of aggregation may give species-area curves that are different from what would be

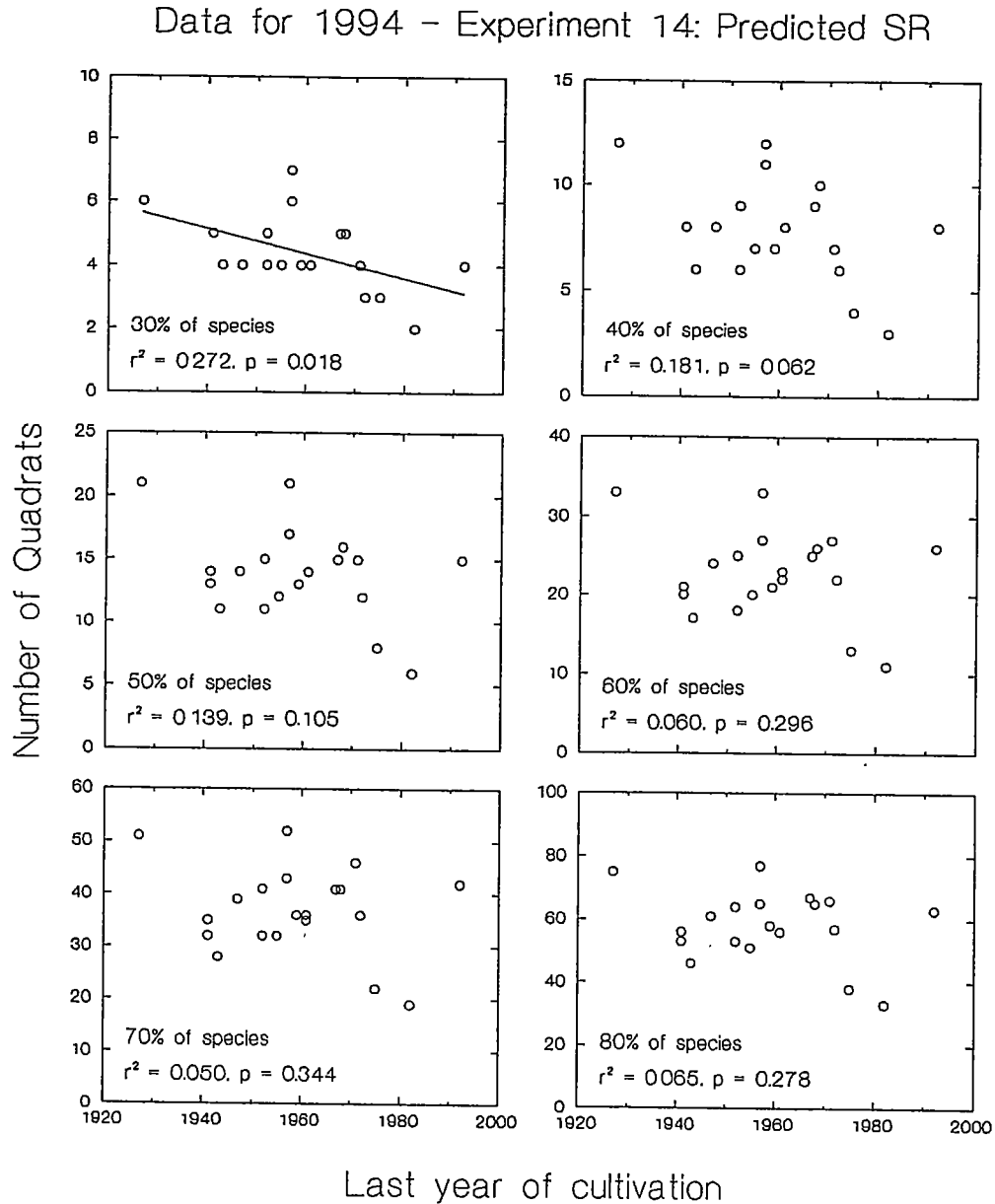


Figure 5. Number of quadrats necessary to observe varying percentages of the estimated field SR in each of 20 old-fields. Each point in each graph represents one old-field. Estimated field SR was calculated by fitting the equation $SR = 1/(A + 1/NPLOTS)$ to values for average cumulative SR.

obtained by randomly locating plots of various sizes, with the differences again being a function of the degree of patchiness or homogeneity in the distribution of species. Where the goal of a study is to obtain a best estimate of total species richness for a discrete area (e.g., an old-field, a reserve, or a reconstructed prairie), a sampling design that maximizes the likelihood of encountering the full range of spatial variation should be the most efficient.

There was some indication that the sampling effort necessary to identify the same proportion of species varied systematically with the time since last cultivation, however this pattern was present only in the 1994 data (Figure 5) and it was statistically significant only for a relatively small proportion of total SR. On balance, the results do not suggest that a larger sampling effort would have been necessary to identify the same proportion of species in older, more species-rich, old-fields, a result that was not anticipated. Thus, even

though observed species richness in these old-fields varied from 25 to 66, and estimated species richness varied almost three-fold, the same intensity of sampling is likely to identify a consistent proportion of species across the entire 55-year successional gradient. This result may be particularly relevant to studies aimed at documenting the success of reestablished grassland or prairie ecosystems.

Acknowledgements

This work was supported by the National Science Foundation Long Term Ecological Research grant at the Cedar Creek Natural History Area, MN, and by the Center for Ecological Research and Education at Idaho State University, and by the Department of Biological Sciences at Idaho State University. I thank the Anatomy and Physiology laboratory instructors for allowing me monopolize their computers.

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