Species-Area Relationship and Plot Size: with Some Examples from South African Vegetation

by

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Abstract

A short review is given of mainly recent literature dealing with the problem of minimal area and plot size for sampling vegetation.

A procedure to determine optimal plot size on the basis of the information content given by different plot sizes is demonstrated on 15 examples from eight different South African veld types.

INTRODUCTION

At the end of the last century in Europe and North America, the first attempts were made to consider vegetation ecologically. This new approach made it neccessary to define fundamental concepts on which the new science was to be based.

Soon a number of "schools" developed, differing in the concept of what vegetation basically is, and what possibilities there are to study and classify vegetation.

The development of the concepts and ideas of these various ecological schools are well documented by Whittaker (1962), McIntosh (1967) and Langford & Buell (1969). Very broadly one may divide the schools on bases of their approach: the individualistic and the classificatory. Schools of the individualistic approach regard variations in vegetation to be continual, although some pattern exists. This pattern can be investigated by sampling the vegetation. Schools of the classificatory approach regard vegetation as being composed of basic units of groups of plant species with sociological relations. These units are usually called communities, and can be classified in a system. Again, by sampling the vegetation, one can investigate these communities.

Most vegetation studies use a plot technique for sampling. A series of plots is layed out over the vegetation, according to a certain principle, and information within these plots is recorded. The plot technique, however, gave rise to a problem, namely, the size of the plot. It was reasoned that a pattern, or community, being composed of plant species, needs a certain area to manifest itself. This area was generally called the "minimal area". For adequate sampling, a plot must be large enough to cover the pattern or community to be investigated, and must, therefore, be at least the size of the "minimal area". On the other hand, in studying vegetation it is important, from the economic point of view, that no effort is wasted in collecting maximum information. Therefore, the ideal plot size will be the one nearest to the "minimal area", giving the most favourable balance between information obtained and effort expended.

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The problem, however, has proved to be in the definition of "minimal area".

The object of this paper is to show in a short review of relevant literature, largely after 1952 when Goodall published his extensive review, that the use of the concept of "minimal area" is impractical, mainly because it is impossible to define. It will be suggested that optimal plot size is a more useful concept, and that this can be expressed in terms of information required. It is clear that large plot sizes give more information but require much effort.

Some examples from South African vegetation types will demonstrate the applicability of this concept.

SPECIES-AREA RELATIONSHIP

In the Braun-Blanquet school of phytosociology the determination of "minimal area" is usually based on the species-area curve. A series of nested quadrats is layed out in a homogeneous piece of vegetation and the increase in number of species in the successively enlarged area is recorded. The number of species is then graphically plotted against the area. In 1913, Braun-Blanquet (quoted in Goodall, 1952, and Hopkins, 1957) defined minimal area (Mindestausmass) as "the area above which no new species occur in the association". Later (1928, 1964) he modified this definition to "the area at which the species-area curve became more or less horizontal." Ellenberg (1956) gives the same definition: "Als Minimal-Areal der Gesellschaft gilt diejenige Flächengrosse, bei der die anfangs steil ansteigende Kurve in den fast waagerecht verlaufenden Ast umbiegt." Recently Tüxen (1970) reinterpreted this curve, regarding it as consisting of three phases: (a) a strongly curved phase; (b) a slanting straight line; and (c) a horizontal line. Minimal area is taken as the area at the point where the horizontal line starts.

It has often been pointed out (for example, Goodall, 1952; Cain & Castro, 1959; Van der Maarel, 1966; Daubenmire, 1968) that on the species area regression curve the point of inflexion depends on the relative scales of abscissa and ordinate axes. Cain & Castro (1959) showed that, depending on the ratio of these axes, they could find three different minimal areas for an American grassland association. They then tried to develop a more accurate and independent method to determine the point of inflexion. A tangent to the curve was constructed, parallel to a line through zero and a point (x, y), where x is 10% of the ultimate area that is surveyed, and y is 10% of the number of species for that area. The tangent "point" gives then the minimal area. This type of method has the great disadvantage, however, as pointed out by Goodall (1952), that the resulting minimal area depends closely on the size of the largest area that is surveyed—the larger this area, the larger the minimal area.

Du Rietz *et al.* (1920) (quoted in Goodall, 1952; Hopkins, 1957) and later again Du Rietz (1954), defined minimal area as the area above which there was no increase in constant species, constant species being those species of a community which have a percentage frequency greater than 90% on an area of sufficient size, that is, above the minimal area. They pointed out that there was a step in the constancy-area curve above which only extremely large areas would add new constant species. Other Scandinavian ecologists, like Nordhagen (1923) and Kylin (1926), doubted this. Nordhagen (1923) argued that the definition of minimal area must be of a practical kind and should be the area that includes all the important constant species, particularly the dominant ones. In his analysis of twelve British plant communities, Hopkins (1955, 1957) came to the conclusion that neither a break in the species-area curves, in the sense of the Braun-Blanquet school, nor a step in the constancy-area curves in the sense of the Uppsala school, can be shown with enough evidence, and thus that a minimal area cannot objectively be defined on these bases. He introduced (Hopkins, 1955) the term

"characteristic area", which can objectively be defined as $\frac{\alpha}{N}$, [where α is the index of diversity, and N the number of individuals ("plant units") on the sample area ("unit area")], but whose ecological meaning is not clear.

Poore (1964) constructed species-area curves for a tropical rainforest in Malaysia and found "little sign of flattening out at large areas." Later (Poore, 1968) he constructed species-area curves from the same data for a number of constant species and for tree species represented by more than ten and twenty trees. Apart from the curve for more then ten trees, which continues to rise, all these curves flattened at about 4 ha. Poore concluded that "if it is considered adequate to define forest types on constant species of large trees, sample areas amounting to between 2 and 5 ha should be large enough."

Van der Maarel (1966) concluded from a detailed study that minimal area cannot satisfactorily be defined as an absolute intrinsic character of the vegetation and, therefore, must be interpreted "pragmatically" as the minimal size of area that must be analysed to get a representative view of a vegetation. The term "representative" is not further defined. He based his practical definition then on frequent species (Van der Maarel, 1966; 1970).

Other definitions by investigators of the Braun-Blanquet school are given by Meyer Drees (1954), who distinguished qualitative and quantitative minimal area for applied survey in tropical rainforests. For qualitative minimal area practically all plant species are present, whereas in the quantitative sense all timber species reach such dimensions that it can serve as a basis for timber estimations. Beeftink (quoted in Van der Maarel, 1966) modified the concept of quantitative minimal area, as the area where all the species present get a rating on a combined abundance-dominance scale that is characteristic of the particular vegetation. Calléja (1962) studied a *Brachypodietum*, relating the increase in the number of species per increase of area $(\wedge v)$

 $\frac{1}{2}$ to the surface area. He thus obtained hyperbolic curves whose parameters he

considered characteristic of the particular vegetation. With this method, it is possible to determine objectively and practically a minimal sample size, but even then only after certain conventions have been adopted, for example, the choice of the system of co-ordinates to be used (Segal, 1969). Calléja found that a community does not have a strict fioristic minimal area. Thus methods of studying minimal area based on species number are inadequate, or subjective, and that apart from floristics the structure of the vegetation should also be taken into account (Calléja, 1962). Gounot & Calléja

(1962) suggested the use of co-efficient of similarity (P = $\frac{c}{a+b} \times 100$, in which a and b

are the number of species in stand A and B respectively, and c is the number of species common to A and B), to define the minimal area, this being the area where the average co-efficient between four samples of the same size is significantly higher than a given value. Again one has to agree on the "given value". Segal (1969) pointed out the importance of taking into account the structure of the vegetation in defining the

minimal area. He distinguished qualitative minimal area, as the area, which even after a progressive increase, at most yields a relatively small increase in the number of species, and representative minimal area, as the smallest area that provides sufficient space for a combination of habitat factors to develop its characteristic vegetation composition and structure both in a qualitative and in a quantitative sense. He added that the practical difficulty of defining representative minimal area is to quantify it and that its estimation is much more subjective than is the case with the qualitative minimal area.

All these definitions, however, do not result in an objective method to determine minimal area. The pragmatic, rather than statistically determined, definitions are based on the fact that an association or community must be well known in its species and structure, before minimal area can be determined. Especially in areas where the vegetation has not yet been described in associations, these concepts of minimal area cannot serve as the basis for determining the optimal plot size.

Arrhenius (1920) (quoted in Gleason, 1922, 1925; Goodall, 1952; Van der Maarel, 1966) was the first worker, who presented a mathematical expression for the relations between number of species and area:

 $\frac{\text{size of area 1}}{\text{size of area 2}} = \left(\frac{\text{number of species in 1}}{\text{number of species in 2}}\right)^n,$

where n is a constant.

Gleason (1922, 1925) showed that this formula does not give a true picture of the relationships, especially in large areas where the number of species to be expected is much too high. Gleason (1925) presented then the formula:

$$\frac{\log B - \log A}{\log C - \log A} = \frac{b - a}{c - a},$$

where A and B are representative parts of area C, and a, b and c are the number of species on these areas respectively. This formula can also be written as:

 $y = a + b \log_e x$,

where y is the number of species to be expected on area x, and a and b are constants (Goodall, 1952). Pidgeon & Ashby (1940) empirically derived a similar equation.

Fisher (Fisher *et al.*, 1943) derived from biological data, which he compared with the logarithmic series, the equation:

$$S = a \log_e \left(1 + \frac{N}{a}\right),$$

where S is the number of species observed, N the number of individuals and a a constant. Except for small areas, this curve fitted well the one produced by Gleason's (1925) equation, as was shown by Williams (1943). Williams (1943, 1944, 1947 a, b, 1950) called a the index of diversity, and he and others (for example, Von Broembsen, 1966) showed that this and similar formulae, and others, derived from this logarithmic series, fit well a wide variety of natural biological situations. Kilburn (1966) presented another formula for species-area relationships:

$$y = \mathbf{k}\mathbf{x}^{z}$$

where y is the number of species in area x, and k and z are constants. The value of k is taken as the number of species in one square metre, thus it should reflect species size, whereas z reflects the species richness of the community. Only on small areas, up to circa 900 m^2 , does this formula fit the observed data.

Without defining the term minimal area, Goodall (1952) pointed out that the size of the minimal area will be smaller when using rectangular plots, than when one uses square or circular plots to survey a vegetation. This is because the sampling variance is usually less between narrow rectangles than between squares or circles of the same area. In a later paper Goodall (1954) argued that if the minimal area is not purely arbitrary, and since the idea of minimal area implies that one is sampling vegetation homogeneous in some sense, it must be reasonable and possible to base it on the concept of homogeneity. Thus he defined minimal area as the smallest sample area for which the expected differences in composition between replicates are independent of their distances apart. Tests done on a very uniform salt marsh vegetation in Southeast Australia and on a semi-desert mallee scrub suggested that a minimal area does not exist, neither for single species, nor for a complete community.

In 1961 Goodall published a paper on pattern and minimal area, defining the latter as the smallest sample for which, for all species, the variation between replicate samples is independent of the distance between them. In this way no minimal area could be determined for mallee scrub in Australia and an Uganda rainforest.

In 1963 after some further studies in Western Australia, he mentioned, however, that it must be admitted that it is possible to find areas of vegetation which may satisfactorily be regarded as homogeneous even by a fairly vigorous test, and that in such areas a minimal area can be identified by appropriate techniques, such as analysis of variance at different spacings. Grid analysis failed to reveal any significant differences in variance at spacings greater than the average diameter of the dominant individuals.

English workers on statistical ecology studied the interrelated problems of pattern, homogeneity and minimal area in vegetation and concluded that there is "no objective significance for the idea of minimal area" (see Greig-Smith *et al.*, 1963; Greig-Smith, 1964; Kershaw, 1964).

We may conclude that an objective definition of minimal area seems impossible.

OPTIMAL PLOT SIZE

The optimal plot size to be used in sampling vegetation for phytosociological studies will be one giving the most favourable balance between information obtained and effort expended, as has already been pointed out. This suggests a pragmatic approach.

The regression equations of Gleason (1925) and Fisher (Fisher *et al.*, 1943) based on the logarithmic series, are generally regarded as best fitting the observed data (see Goodall, 1952; Hopkins, 1955; Dahl, 1957; Von Broembsen, 1962). The ratio of increase of information (here the increase of species per area) to increase of time needed to survey that area, was used by Scheepers (1968) to determine the most efficient plot size in a survey of the Highveld. The amount of time necessary to sample a plot is not an intrinsic character of the vegetation, however, and will depend on a number of factors. It will vary from observer to observer and from day to day, due to factors such as wind, rain, temperature and topography. Time measurement is, therefore, rejected here as a means for determining plot size.

In 1943 Williams plotted the number of species against the size of the area in which they occurred, both on a logarithmic scale, for areas from as small as 1 cm^2 up to the total landsurface of the earth using check lists and floras. He found that up to an area of circa one hectare the curve "follows the expected increase in species due to

increase in size of sample within a uniform population, or within a single ecological association. In other words, neither the climate nor the rest of the environment changes very rapidly on an average," within an area of this size. "As soon as we pass beyond this limit we begin to include new ecological conditions in our sample, with the result that the number of species will increase more rapidly than would be expected if the population sampled remained uniform."

Thus on the average an uniform population or community can manifest itself within an area of about one hectare and this area can thus be regarded as giving the typical species and structure of the community.

It would be very uneconomic to sample vegetation by means of plots of one hectare*, apart from the fact that in most cases it is difficult to find a reasonably homogeneous area of that size. With the regression equation:

 $y = a + b \log_e x$

(Gleason, 1925; Goodall, 1952), where a and b will be calculated from observed data, the expected number of species in one hectare of the sampled vegetation can be calculated. Regarding number of species as amount of information, the 1 ha value can be taken as the 100% level of information. Arbitrarily and individually one can then decide, what percentage of information one requires per plot, depending, for example, on the scale of the survey, and so calculate the required plot size.

Some Examples from South African Vegetation

Fifteen samples were taken in eight South African Veld Types (Acocks, 1953) in order to test whether this procedure helps to determine optimal plot size. Twelve samples were taken in concentric circles with successive increase in radius (0, 5; 1; 2; 3; 4; 6; 8; 12; 16; 20 m) i.e. the plot sizes varied between $0, 8 \text{ m}^2$ and $1 256 \text{ m}^2$. Three samples in Fynbos vegetation were taken with rectangular nested quadrats of respecively 1; 2; 4; 8; 16; 32; 64; 128 and 256 m². Care was taken that the plots covered vegetation where the physiographic features and the vegetation structure were as homogeneous as possible. The importance of ecological homogeneity in this type of studies was emphasized by Dahl (1957). Every time the increase in number of species of permanently recognizable plants was noted. The samples were spread as follows:

- Sample 1.—Riverine woodland; along Orange River at Goedemoed. Total cover estimated at 95%; tree layer up to 8 m, shrub layer up to 4 m, undergrowth up to 0,30 m.
- Sample 2.—*Themeda*—*Festuca* Alpine Veld (Veld Type 58); in dense grassland about 16 km from Jouberts Pass near Lady Grey. Total cover estimated at 95%; soil loamy; very gentle slope $(\pm 3^\circ)$; aspect SSW; one stratum up to 0,40 m.
- Sample 3.—Dry Cymbopogon—Themeda Veld (50); in grassland near Morgenzon, between Lady Grey and Aliwal North. Total cover estimated at 40%; soil sandy; gentle slope (±5°); aspect SSW; Elyonurus argenteus, Cymbopogon plurinodus, Themeda triandra and other grasses dominant.
- Sample 4.—False Arid Karoo (35); in open dwarfscrub near Kraankuil. Soil loamy sand; on plain. One stratum up to 0, 50 m; *Pentzia incana* dominant.
- Sample 5.—Central Upper Karoo (27); open dwarf scrub near Houtkraal north of De Aar. On calcrete rich plain. One stratum up to 0,45 m; *Pentzia incana* dominant.

^{*} In tropical rainforest one could use plots larger than one hectare, which are then usually sampled by means of subplots. The problem still remains to determine the optimal size of the subplot.

- Sample 6.—False Upper Karoo (36); in open dwarf scrub about 24 km from Norvals pont on way to Bethulie. Total cover estimated at 25%; dwarf shrub layer up to 0,40 m; layer of annuals, rosette plants, etc., up to 0,06 m; *Chrysocoma tenuifolia* dominant.
- Sample 7.—False Upper Karoo (36); in open dwarf scrub about 13 km West of Bethulie. Total cover estimated at 60%; dwarf shrub layer up to 0,40 m; layer of annuals, rosettes, etc. up to 0,10 m; *Chrysocoma tenuifolia* dominant.
- Sample 8.—False Upper Karoo (36); in open shrub and dwarf shrub vegetation at Tussen die Riviere near Bethulie. Total cover estimated at 30%; on dolerite; slope 15°; aspect SSE; dwarf shrub and grass stratum up to 0,30 m; shrub stratum up to 2,50 m; tree ±6 m. Chrysocoma tenuifolia, Rhus ciliata and Rhus erosa dominant.
- Sample 9.—False Upper Karoo (36); in open scrub between Petrusville and Colesberg. Total cover estimated at 65%; on fine-grained sandstone and mudstone; slope 25°; aspect WSW; dwarf shrub and grass stratum up to 0,90 m; shrub stratum up to 4 m. *Rhus undulata* and *Euclea crispa* dominant.
- Sample 10.—False Orange River Broken Veld (40); in open dwarf shrub vegetation near old road bridge across Orange River at Hopetown. Total cover estimated at 35%; on andesitic lava; slope 14°; aspect ESE; dwarf shrub and grass layer up to 0,40 m; very sparse shrub layer up to 2,5 m; *Chrysocoma tenuifolia* dominant.
- Sample 11.—False Orange River Broken Veld (40); in open scrub-dwarf scrub between Hopetown and Douglas. Total cover estimated at 30%; on andesitic lava; on plain; dwarf shrub and grass layer up to 0,50 m; shrub and low tree layer up to 3 m. Acacia mellifera subsp. detinens and Rhigozum trichotomum dominant.
- Sample 12.—Orange River Broken Veld (32); in open scrub-dwarf scrub, about 32 km from Douglas on way to Prieska. On andesitic lava with slight sand cover; on plain; dwarf shrub and grass layer up to 0,50 m; shrub layer up to 4 m. Acacia mellifera subsp. detinens and Phaeoptilum spinosum dominant.
- Sample 13.—Fynbos (69); in dense *Protea neriifolia*—*Protea repens* scrub at Jonkershoek near Stellenbosch. Total cover estimated at 100%; on Table Mountain sandstone; slope 24°; aspect E; undergrowth up to 0,50 m; shrub layer up to 3 m.
- Sample 14.—Fynbos (69); in *Protea arborea* pseudo-savannah at Jonkershoek near Stellenbosch. Total cover estimated at 95%. on Table Mountain sandstone; slope 36°; aspect N; undergrowth up to 0,60 m; tree layer up to 4 m.
- Sample 15.—Fynbos (69); in dense Restionaceous vegetation at Jonkershoek near Stellenbosch. Total cover estimated at 95%; on granite; slope 32°; aspect SE; one vegetation layer up to 0,60 m with isolated emergents up to 2 m.

Table 1 shows the observed numbers of species of each plot at different plot sizes, the calculated constants a and b of the expression $y = a + b \log_e x$, and the expected number of species in 1 ha of the population. Calculated values for number of species fitted the observed values closely for the different plot sizes, indicating that reasonably homogeneous populations were sampled.

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TABLE 1

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Taking the calculated number of species in 1 ha of the population as the 100% level of information, the plot sizes belonging to respectively the 40%, 50%, 55%, 60% and 70% levels of information were calculated. The results are shown in Table 2.

C	Veldtype	Plot size in m^2 for $\frac{0}{10}$ of ha-information				
Sample		40%	50%	55%	60%	70%
1	RW	8,3	26,9	48,6	99,0	287
2	58	2,8	10,9	21,6	42,6	167
3	50	3,0	11,5	22,7	44,6	173
4	35	15,4	45,3	77,7	133,0	392
5	27	19,7	55,6	93,5	157,0	444
6	36	9,4	30,1	53,8	96,2	307
7	36	7,6	25,0	45,5	82,9	274
8	36	27,6	73,7	120,0	197,0	525
9	36	31,0	81,3	132,0	212,0	557
10	40	9,6	30,5	54,4	97,1	309
11	40	11,5	35,6	62,5	110,0	339
12	32	24,2	66,0	109.0	181.0	492
13	69	9.9	31.4	56.0	99.6	315
14	69	27,3	73.0	119.0	195.0	522
15	69	17,8	51.3	86.9	147.0	423

TABLE 2

Comparing the two grassland samples from the *Themeda—Festuca* Alpine Veld (sample 2) and the dry *Cymbopogon—Themeda Veld* (sample 3) with the two dwarf scrub samples from the False Upper Karoo (samples 6 and 7) at the 40% level, it is necessary in karoid dwarf scrub to have a plot of about three times that in grassland in order to get the same amount of information. At the 60% level this value has become about two times. The same features are shown by comparing the two dwarf scrub False Upper Karoo samples (6 and 7) with the two open tall scrub and tree amples from the same Veld Type (8 and 9).

These differences are probably mainly due to the structure of the vegetation types. In a tall scrub and tree vegetation a number of plants have larger dimensions than in a dwarf scrub vegetation, thus the average plant interspacing is necessarily larger. The same applies to differences between dwarf scrub and grass vegetation types, although here the Karoo dwarf scrub vegetation is also usually more open than the Highveld grasslands.

Similar results were shown when the procedure was tested on a set of nested quadrats from 1 to 1 024 m², taken by Mr. J. C. Scheepers in Transitional *Cymbopogon—Themeda* Veld (49) near Kroonstad in an overgrazed, trampled, harvester termite infested, patchily denuded grassland. The number of species expected on one hectare of this grassland (52,7) compares well with the values of the other grasslands (samples 2 and 3; Table 1). Much larger plot sizes are necessary for this grassland than for the two others, however, to get a similar percentage of information (for 40% of ha-information 24,7 m², for 50% 67,3 m², for 55% 110,1 m²). These results show, that although the pattern in the grassland is similar to other grasslands, the structure is much coarser here, and one should sample it with much larger plots due to the patchily denuded veld.

The importance of the structural factor for plot size and minimal area have already been pointed out by Calléja (1962), Gounot & Calléja (1962), Segal (1969) and others.

Values for the False Arid Karoo and the Central Upper Karoo samples (4 and 5) are intermediate between the dwarf scrub (samples 6 and 7) and tall scrub and tree samples (samples 8 and 9) of the False Upper Karoo. Values for the False Orange River Broken Veld (10 and 11) compare well with the dwarf scrub of the False Upper Karoo (6 and 7) and values for the Orange River Broken Veld (12) with the tall scrub of the False Upper Karoo (8 and 9). Also, values for the open *Protea arborea* vegetation (Fynbos; sample 14) compare well with the tall scrub of the False Upper Karoo (8 and 9). Those for the *Protea neriifolia—Protea repens* scrub (sample 13) agree better with the dwarf scrub values from the False Upper Karoo (6 and 7), whereas the values for the Restionaceous vegetation (sample 15) compare with those of the False Arid Karoo (4) and Central Upper Karoo (5).

Of course, structure of the vegetation is not the only important factor. Floristic richness is also important. The sample from the riverine woodland (sample 1) shows values comparable with those of dwarf scrub False Upper Karoo (6 and 7) vegetation, although its structure is much coarser than these. This is probably due to the floristic poorness of the riverine woodland. On a rather small area most of the species are already present, and very few new ones appear on larger areas.

The structure of the vegetation of sample 15 is comparable with those of the grasslands (2 and 3). Still, in sample 15 a much larger plot size, similar to the False Arid and Central Upper Karoo, is needed to get an equal percentage of information. The floristic richness of the Restionaceous vegetation can be regarded as the main factor for this phenomenon.

Although this approach does not give a specific value for an optimal plot size for a certain type of vegetation, it allows one to form an idea of the percentage information obtained with different plot sizes. One can then decide arbitrarily what increase in information is worth the extra effort needed to sample a larger plot.

Arbitrarily, the author has regarded the optimum plot size as between 50% and 55% of the hectare-information for a phytosociological survey of the Orange River Valley.

If one reckons that an area of one hectare is insufficient for a certain community to manifest itself, one can calculate in the same way the expected number of species for any size area that is regarded as sufficient. The same procedure can then be followed for determining the optimal plot size.

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