

THE SPECIES-AREA RELATION II. A SECOND MODEL FOR CONTINUOUS SAMPLING¹

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INTRODUCTION

In the previous paper dealing with a model of the species-area relation for discrete sampling (KOBAYASHI, 1974), it was shown that the number of species occurring in a given number of quadrats can be predicted by a simple mathematical model if a certain area is chosen as the quadrat size. In this case, however, it was pointed out that since the quantity representing sample size is essentially continuous, another model should be constructed for continuous expanding of sample area. The purpose of this paper is to build a second model describing the species-area relation for continuous sampling and to make clear the implication of parameters involved.

MODELING

The model of species-area relation for discrete random samples showed that regardless of quadrat size, if each component species is distributed in negative or no association with one another, the number of species (θ_n) newly added in n th quadrat approaches to

$$\theta_n \propto \frac{1}{n} \quad (1)$$

as n increases (KOBAYASHI, 1974). A similar relation may be expected also for continuous expanding of sample area if individuals or clusters of individuals in each species are distributed at random throughout a homogeneous habitat.

Provided that a sample area (x) corresponds to n quadrats each being Δx in size, then putting $\theta_n = \Delta S$, we can rewrite the equation (1) as

$$\Delta S \propto \frac{1}{n} = \frac{\Delta x}{n \cdot \Delta x} = \frac{\Delta x}{x} \quad (2)$$

That is, if x is fully large, the increment (ΔS) in the number of species is proportional to the increment (Δx) in the sample area and inversely proportional to the total area (x) sampled. The relation (2) shows that $\Delta S \rightarrow \infty$ as $x \rightarrow 0$. This can not be the case because ΔS must have a finite value. Then we write as

$$[\Delta S]_{x=0} \propto \frac{\Delta x}{E} \quad (3)$$

where E is a constant.

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Combining the relations (2) and (3), we have

$$\Delta S \propto \frac{\Delta x}{E+x},$$

whence the rate of increase (dS/dx) in the number of species is expressed as

$$\frac{dS}{dx} = \frac{A}{E+x} \quad (4)$$

where A is a proportional constant. The differential equation (4) represents a mathematical model describing the species-area relation for continuous sampling.

Let $S=0$ at $x=0$, the solution of (4) is

$$S = A \ln \left(1 + \frac{x}{E}\right)$$

(throughout this paper the natural and the common logarithms are denoted by \ln and \log respectively).

The above equation shows that $S=A$ at $x=(e-1)E$ where e is the base of natural logarithms. As will be shown later, the area $(e-1)E$ corresponds to the characteristic area previously proposed (KOBAYASHI, 1974), so that it follows

$$A = \lambda$$

where λ denotes the number of species occurring in the characteristic area. Then the final form of the model is

$$S = \lambda \ln \left(1 + \frac{x}{E}\right). \quad (5)$$

If λ and E are replaced by α and α/ρ respectively, the equation (5) becomes identical with the logarithmic series distribution proposed by FISHER *et al.* (1943):

$$S = \alpha \ln \left(1 + \rho x / \alpha\right) \quad (6)$$

where α is the index of diversity and ρ the number of individuals per unit area.

APPLICATION OF THE MODEL

The equation (6) has already been applied to plant communities by WILLIAMS (1950) and HOPKINS (1955): The fit was good for larger area, but HOPKINS noticed the consistent discrepancy in smaller area. Since all visible plants such as Spermatophyta, Pteridophyta, Bryophyta and Lichens were recorded in these cases, the data mingled them may include two or more groups of species each having different values of λ and E . Such records have been rather common to treatises on the species-area relation of plant communities (e.g., ARCHIBALD, 1949a and 1949b; KILBURN, 1966). As has been pointed out, the equation (5) is the relation expected for a group of species characterized by λ and E , so that it is quite possible that the discrepancy between observed and expected plots arises from indiscrimination of the groups of species each having different λ and E . All data of the sort ought to be rearranged for testing availability of the equation (5).

Fig. 1 shows the result applied the equation (5) to the data of Wisconsin jack pine stand (KILBURN, 1966). At first the equation was fitted for the group of

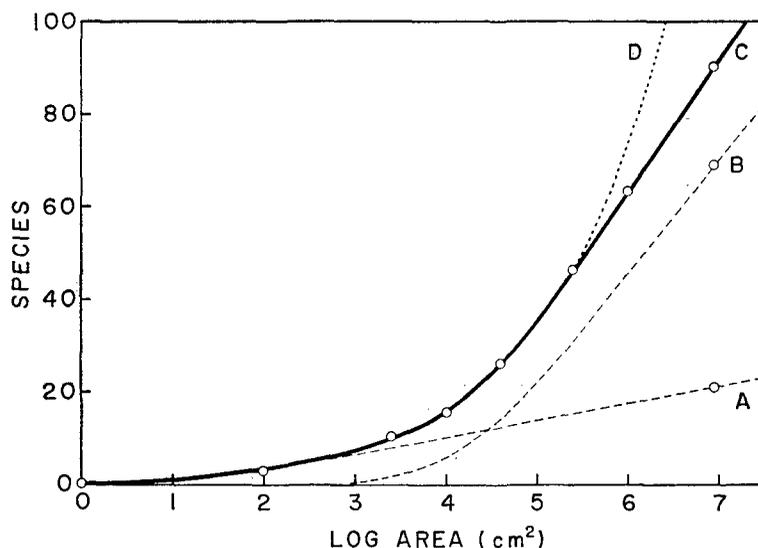


Fig. 1. Species-area relation for the jack pine woodland (Data from KILBURN, 1966). A is the individual curve for bryophytes and lichens, $S_1=3.7 \log (1+x/17)$; B is the one for vascular plants, $S_2=24.2 \log \{1+x/(1.4 \times 10^4)\}$. C denotes the compound curve of A and B, $S=S_1+S_2$; D is the parabola fitted by KILBURN, $S=16x^{0.33}$.

vascular plants and for that of bryophytes and lichens separately, because they are apparently of different synusiae each having different λ and E : As the original data did not present these groups separately except for the area of 900m^2 , the individual curves were fitted by eye through the points of 69 species for the vascular plants and 21 species for the bryophytes and the lichens at 900m^2 . Namely, the tangent to the observed curve through the point $S=21$ and $\log x=6.954$ ($x=900 \times 10^4 \text{cm}^2$) was drawn by eye. The slope of the tangent gave $\lambda_1=3.7$ (against the common logarithm of area), and the intersection of the tangent and the abscissa gave $E_1=17$. Next, by subtracting the values of $S_1=3.7 \log (1+\frac{x}{17})$ from the observed number of species, $\lambda_2=24.2$ (against the common logarithm of area) was found from the slope of the linear part of the remained curve, and $E_2=1.4 \times 10^4$ from the intersection of the backward projection of the linear part and the abscissa. The compound curve of them (S_1+S_2) was then compared with the actual plots. As will be seen in Fig.1, the theoretical curve is in good agreement with the observed values. If it is possible to split the synusiae more minutely, the result will be improved further.

Other examples of the species-area relation compared with the theoretical curve are given in Fig. 2 in which the data by HOPKINS (1955) are used. It should be noticed that these plant communities are assumed to comprise at least two or three synusiae. The curves expected for the individual synusiae were fitted by eye because

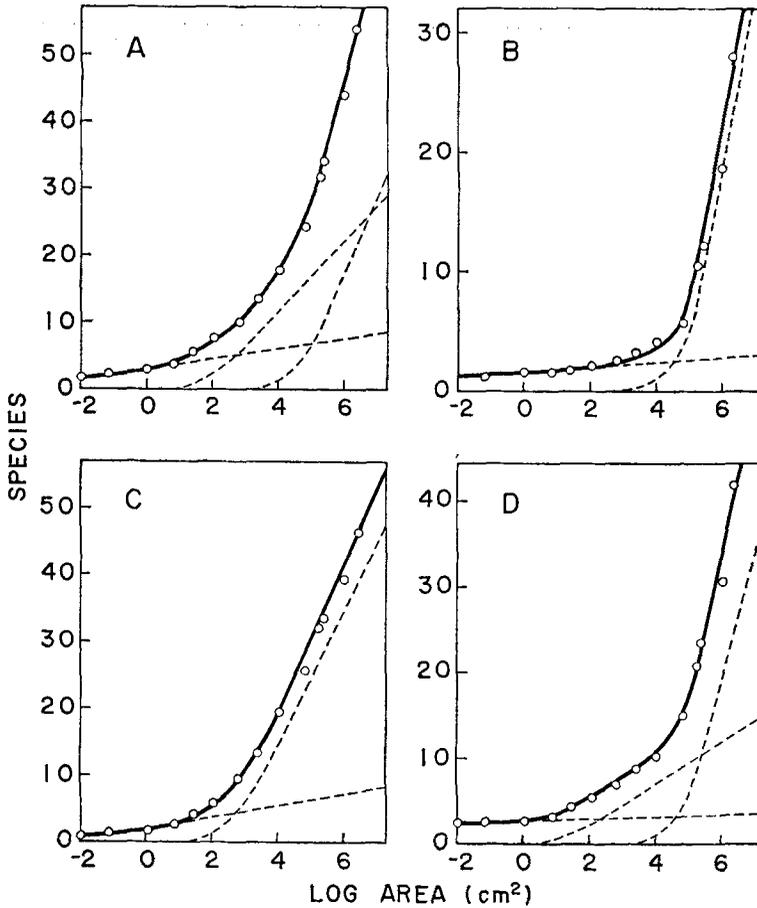


Fig. 2. Species-area relations for plant communities (Data from HOPKINS, 1955). A: Wrynose grassland, B: Hillock wood, C: Mayo bog and D: Rannoch wood. The broken lines show the individual curves for a single synusia, and the thick solid lines show the curves compounded them. A and D are assumed to comprise three synusiae, and B and C two synusiae.

it was impossible to point out which species belongs to which synusia. The method of finding the value of parameters is virtually the same as stated in the case of Wisconsin jack pine stand. In this case, however, no data were given for each synusia, so that each value of the parameters was chosen by successive approximation so as to give the least number of synusiae. In Fig. 2 it will again be seen that every compound curve indicates goodness of fit in the whole extent of the area sampled.

ECOLOGICAL IMPLICATION OF THE PARAMETERS

The species-area relation for j groups of species, each having different values of λ and E , can be written as

$$S = \sum_{i=1}^j \lambda_i \ln(1 + x/E_i) \quad (7)$$

where $i=1, 2, 3, \dots, j$. This expression has already been given by ANSCOMBE (1950).

Then the index of diversity proposed by WILLIAMS (1943) will be approximated by

$$\alpha = \sum_{i=1}^j \lambda_i$$

in larger area, because 1 is negligible as compared with x/E if x is large, so that

$$S \approx \sum \lambda_i \ln(x/E_i) = (\sum \lambda_i) \ln x - \sum (\lambda_i \ln E_i),$$

while the equation (6) can be written as

$$S \approx \alpha \ln(\rho x/\alpha) = \alpha \ln x - \alpha \ln(\alpha/\rho)$$

if x is large.

Since λ means the number of species occurring in its characteristic area $(e-1)E$, the value of λ is independent of sample size. As is expected theoretically, the more species an area contains, the larger the value of λ becomes. Thus, as the value of λ shifts from zero to infinity with increasing species richness, it will be a valid measure of species diversity. We will call it *specific diversity*. An advantage in its practical use may be that its theoretical implication is so obvious that it can be used as an analytical tool *per se* in the study of biotic communities.

Another parameter E pertaining to the equation (5) indicates the area given by intersection of the abscissa and the backward projection of linear part of the curve as pointed out by HOPKINS (1955). Since its value decides the position shifting from the first gentle slope to the next steep in the curve with expanding area, E may be considered a parameter characterizing factor(s) that control spatial segregation of species in smaller area, while λ mainly controls slope of the curve in larger area. The factors that affect the value of E may be enumerated as follows :

(1) The value of λ : If the mean number of individuals in a unit area is ρ , the following relation always holds

$$\lambda \leq \rho (e-1) E,$$

because the number of species in a given area does not exceed the number of individuals in the area. That is, E depends on λ if ρ is constant.

(2) The density of individuals: As is shown by the above equation, E depends on ρ if λ is constant.

(3) The size of individuals : If each individual is so large in size that it occupies a wide area, ρ becomes small. Therefore E depends on the size of individuals.

(4) The degree of aggregation in the individuals of each species : Provided that the individuals of i th species are distributed following a negative binomial, the frequency at the area $(e-1)E$ is written as

$$F_i = 1 - \{1 + \rho_i (e-1) E/k_i\}^{-k_i}$$

where k_i is a constant reflecting the degree of aggregation. Since λ is the sum of F_i for all the species which may occur in a habitat, E depends on k_i if λ and ρ_i is constant.

(5) The interspecific association : If each species is distributed separately from the others, i. e., their individuals are distributed in clumps or in interspecific territories, we would not encounter another species until we cover the clump or the territory.

That is, E would become large. On the contrary, if the individuals of every species are ubiquitously distributed in a habitat each being mingled with other species, we would encounter another species almost at every individual. That is, E would be small.

As E thus depends on the size of individual and the ecology of species, we may regard it as an index characterizing a "synusia" which has been termed a group of species consisting of one or few closely related life forms occurring together and having a similar ecology (CAIN and CASTRO, 1959). For example, such small plants as mosses and lichens will show smaller value of E , while such large plants as trees and shrubs will show larger value. It may therefore be said that the equation (5) holds only among the species belonging to a synusia. POORE (1962) has correctly pointed out that the description of phytocoenose (=plant community) should be made in terms of its synusiae and these should be sampled separately, because each synusia has different parameters reflecting their ecology.

In this context, if the spatial structure of a synusia can be regarded as a mosaic whose component pieces (so to speak, patches) are each occupied by a species, the value of E may reflect the size of component patches in the mosaic structure of synusia: If the size of patches is large the constituent species will be segregated from one another and this results in long continuation of first gentle slope in the species-log area curve, while if it is small they will be less segregated from one another and this results in quick rise of the curve. As E is thus related to the size of component patches in a mosaic, it will be named the *elemental area*. HOPKINS (1955) has suggested that the value of E (α/N in his term) may be regarded as an objectively defined area of a plant community, but has encountered a difficulty in interpreting its ecological significance. This difficulty may be due to the application of a single logarithmic equation to a community which includes two or more synusiae.

In an elemental area E , the expected number of species (S_E) is given by $\lambda \ln 2$. Then if λ is larger than $1/\ln 2 = 1.443$ (that is, the area is rich in species) S_E is larger than unity. This may imply that we encounter more than one species within the elemental area, and that the patches of different species are partly overlapped one another. Conversely, if λ is smaller than $1/\ln 2$ (that is, the area is poor in species) S_E is smaller than unity. This may imply that we will have to cover more than the elemental area in order to encounter one species, and that the area of gap where plant (or animal) is absent is large compared with the area of patch where it is present. The former case may be seen in a tree layer in which the canopies of each tree are more or less mingled with one another when they are distributed without gap. The latter case may be seen in a ground surface layer in which small plants are scattered sparsely.

In this connection, the area required to encounter one species on an average (hE) may be regarded as the mean size of patches. This is closely related to the "mean

area" (not of a species but of a synusia) defined as the reciprocal of density by KYLIN (1926), because occurrence of one individual corresponds to that of one species. With the value of hE we may roughly assess the number of individuals in a given area.

The value of h is as follows: If $S=1$, the equation (5) becomes

$$1 = \lambda \ln(1 + x/E)$$

or $x = (e^{1/\lambda} - 1)E,$

so that $h = e^{1/\lambda} - 1.$ (8)

The case where $h=1$ (viz., $\lambda=1/\ln 2$) may be regarded as a standard of species diversity, since in this case the values of hE and E are equivalent, and doubling the area adds one new species to the total in larger area. Hereafter hE will be referred to as the *specific area*. Furthermore, if we use the number of individuals (N) pooled all species instead of the area (x), it follows

$$S \approx \lambda \ln(1 + hN),$$
 (9)

since $x/(hE) \approx N.$

This equation shows a model for the species-individual relation.

These parameters of the synusiae in several plant communities shown in Fig. 2 are tabulated in Table 1 (for the method of finding these values, see p. 267). For the lowest synusia of Rannoch wood, the values of E , hE and C were exceedingly small ($E=1.0 \times 10^{-21}$, $hE=4.9 \times 10^{-14}$ and $C=1.7 \times 10^{-21}$ cm). This is due to the fact that the ground flora was so luxuriant that 2.4 species occurred even in the area of 1 mm^2 (HOPKINS, 1955). Judging from the result that the value of λ in this synusia approximates zero, the species belonging to the synusia (two species of *Vaccinium* and two species

Table 1. Parameters for the plant communities
(Data from HOPKINS, 1955).

Community	Specific diversity λ	Elemental area $E \text{ cm}^2$	Specific area $hE \text{ cm}^2$	Characteristic area $C \text{ cm}^2$
Mayo bog	0.35	1.0×10^{-3}	1.7×10^{-2}	1.7×10^{-3}
	4.13	3.2×10^2	8.8×10	5.4×10^2
Hillock wood	0.09	1.0×10^{-8}	1.5×10^{-6}	1.7×10^{-8}
	5.22	4.0×10^4	8.5×10^3	6.8×10^4
Wrynose grassland	0.30	2.0×10^{-3}	5.2×10^{-2}	3.4×10^{-3}
	2.22	5.8	3.3	9.8
	4.13	2.3×10^4	6.3×10^3	3.9×10^4
Rannoch wood	0.04	*	*	*
	1.00	1.1×10	1.9×10	1.9×10
	5.57	4.4×10^4	8.7×10^3	7.5×10^4

$$h = e^{1/\lambda} - 1, C = (e - 1) E.$$

* For this synusia, see text.

of Bryophyta) may be exceptional in their coverage.

Although these synusiae were temporarily discriminated in each community, it should be pointed out that λ increases with the increase of E . This relation appears to be quite clear and is of interest with regard to the species diversity, but it may be safe to refrain from further comment on this relation since the information is not sufficient to confirm whether or not these individual values represent true synusia.

THE CHARACTERISTIC AREA OF A SYNUSIA

It may also be worth while examining the concept of "minimal area" or "representative area". According to HOPKINS (1957) the minimal area has been defined as the area above which the species-area or the constancy-area curve becomes approximately horizontal (constancy means the number of "constants" being defined as species which have a frequency larger than 90 per cent). Complying with this definition, PRESTON (1962) has concluded that the locus of break in a species-area curve is given by the point of maximum curvature, and has demonstrated this point for the parabolic species-area curve. However, since most of the observed curve can not be expressed by such simple form as parabola, the difficulty with this is that it is almost impossible to determine mathematically the point of maximum curvature.

Thus the minimal area defined from the form of species-area curve seems not to be worth mentioning. Apart from the minimal or the representative area, it may be possible to define another area which is characteristic of a biotic community: In the previous paper (KOBAYASHI, 1974), the characteristic area C was defined based on the idea that the species-area relation is expressed by a simple mathematical equation when a certain area is chosen as a unit size of sampling. That is, if the size of sampling unit is equal to C , the number of species (S_n) occurring in n samples is given by

$$S_n = \lambda \Sigma (1/n) \quad (10)$$

where $\Sigma (1/n)$ shows an abbreviation for $\sum_{r=1}^n \frac{1}{r}$, and when the size of sampling unit differs slightly from C , the relation between S_n and n is approximated by

$$S_n = u + v \Sigma (1/n) \quad (11)$$

where u and v are constants.

According to this consideration, when the number of species occurring in the area nx ($n=1, 2, 3, \dots$) satisfies the equation (10), the area x should be equal to C . To find this value of x , we set up an equation

$$\lambda \Sigma (1/n) = A \ln (1 + nx/E).$$

Since λ is the number of species at $n=1$, that is, $\lambda = A \ln (1 + x/E)$, the above equation can be rewritten as

$$\Sigma (1/n) = \frac{\ln(1 + nx/E)}{\ln(1 + x/E)}. \quad (12)$$

Then the value of x satisfying the equation (12) will give the characteristic area.

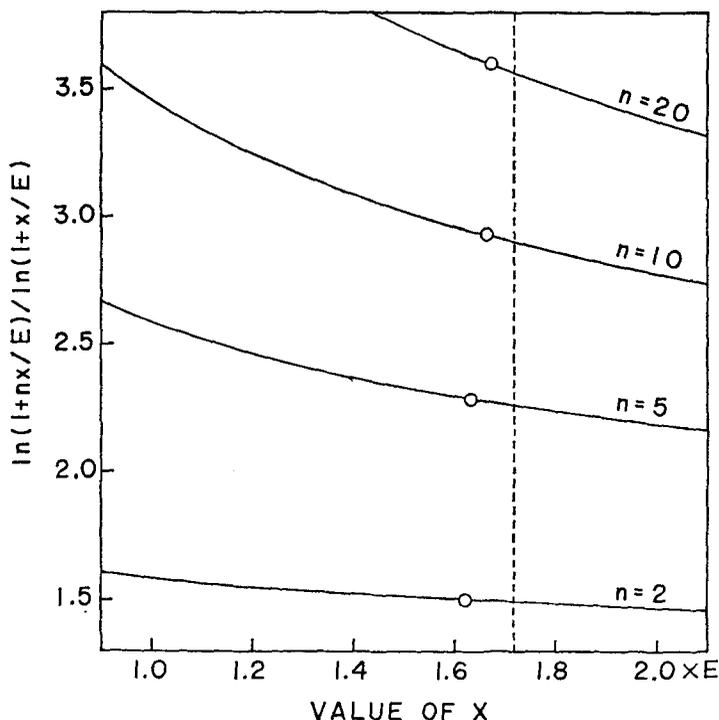


Fig. 3. Relation between $\ln(1+nx/E)/\ln(1+x/E)$ and x expressed in terms of E at $n=2, 5, 10$ and 20 . The open circle on each curve shows the value of $\Sigma(1/n)$, and the broken vertical line shows $x=(e-1)E$.

In Fig. 3 the values of right-hand side of the equation (12) are plotted against different value of x in terms of the elemental area (E) at $n=2, 5, 10$ and 20 . Although the value of x satisfying the equation (12) increases slightly with the increase of n as will be seen from Fig. 3, it is likely to show nearly the same value. If we assign $(e-1)E$ to an approximate value of x satisfying the equation (12), it follows that

$$\frac{\ln(1+nx/E)}{\ln(1+x/E)} = \ln\{1+n(e-1)\},$$

which gives the fairly good approximation of $\Sigma(1/n)$ at any value of n (the difference between $\Sigma(1/n)$ and $\ln\{1+n(e-1)\}$ shows the maximum, $\gamma - \ln(e-1) \approx 0.036$, at $n=\infty$ where γ is EULER'S constant). From this it may be said that the characteristic area C is approximated by $(e-1)E$. In this area C the value of specific density is equal to λ because $S = \lambda \ln e$.

The values of $(e-1)E$ calculated tentatively for plant communities are exemplified in the right-hand column of Table 1. Since the characteristic area defined as $C = (e-1)E$ depends only on the parameter of synusia and denotes the size of sampling unit only with which the probability of encountering new species in n th sample is reflected by the number of samples (n), it can also be regarded as an intrinsic property of synusia. It may then be concluded that the equation (10) or (11) for the discrete

sampling is also valid only for a single synusia.

RELATIONSHIP BETWEEN DISCRETE SAMPLING AND CONTINUOUS SAMPLING

GOODALL (1952) has stated that it is hopeless to find means of converting results obtained by discrete sampling to those which would have been obtained from continuous sampling. As has been mentioned, however, the equation (10) can be regarded as a special case of the equation (5). This suggests the possibility of conversion from one to another if the result by the discrete sampling does represent the spatial distribution of individuals in each species as it is. Since the equation (5) provides the number of species occurring in any size of quadrat, it will be possible to predict the result which will be obtained by combining discrete samples at any level of quadrat size. Conversely, the data obtained by discrete sampling will be applicable to the equation (5) only on the assumption that the distribution of individuals in each sample reflects the true spatial distribution of them.

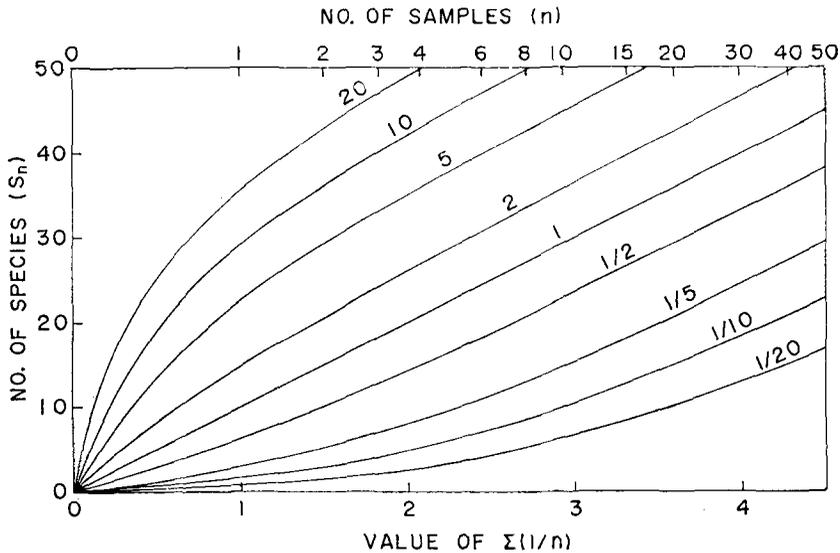


Fig. 4. Relation between the number of species (S_n) and the value of $\Sigma(1/n)$ at different sizes of sampling unit in a hypothetical synusia having $\lambda=10$ and $E=1/(e-1)$. The numerals in the figure show the size of sampling unit.

Fig. 4 shows the relation between S_n and n for the discrete samples taken from a hypothetical synusia which follows the equation (5) with the parameters $\lambda=10$ and $E=1/(e-1)$. As will be seen from this figure, if the quadrat size is equal to the characteristic area $C=1$, the relation of S_n to $\Sigma(1/n)$ is linear and fits the equation (10); while if the quadrat size deviates from C , the relation of S_n to $\Sigma(1/n)$ is curvilinear and fits approximately the equation (11) for larger n .

Since the equation (11) is thus regarded as an approximate expression in the case where the size of sampling unit deviates from C , we may instead use the equation (5) substituting the continuous quantity (x) for the discrete (n), assuming that the spatial distribution of individuals in each species was not distorted by the discrete sampling.

Fig. 5A shows the result of fitting the equation (5) to the data of tall-grass prairie (RICE and KELTING, 1955) which has been illustrated in Fig. 4 of the previous paper (KOBAYASHI, 1974). Since the data were taken by the use of 100 quadrats of 1000cm^2 , we can easily substitute x for n . The fitted equation is

$$S = 13.7 \ln(1 + x/3172) \\ = 31.5 \log(1 + x/3172)$$

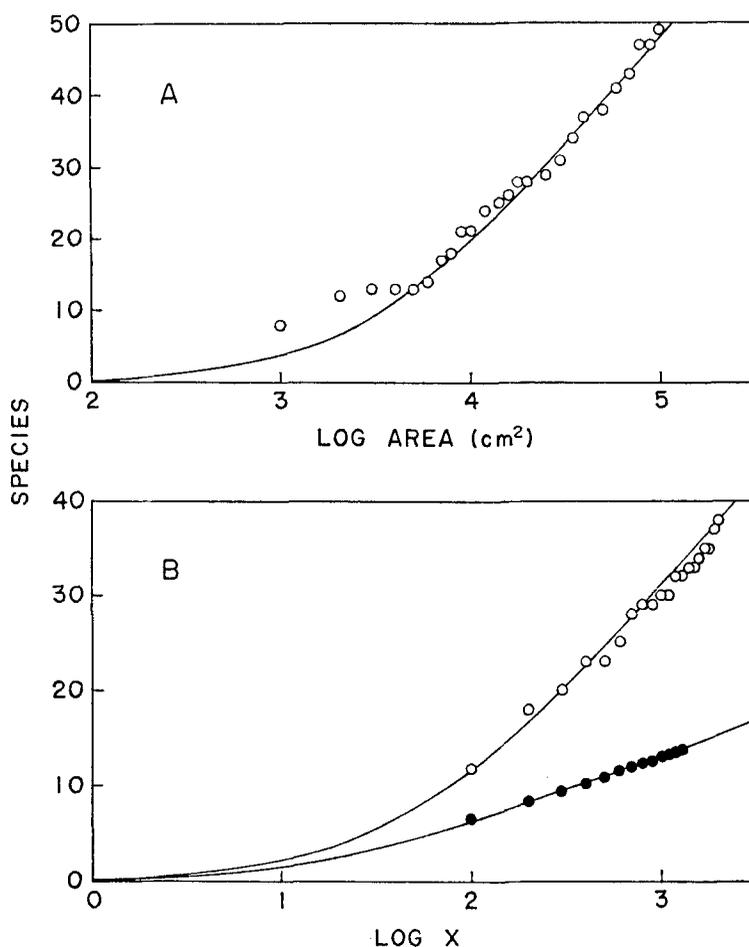


Fig. 5. Fitness of the equation (5) to the data obtained by discrete sampling. A: plants in a tall-grass prairie (some observed plots above 10^4 cm^2 are omitted in the figure), B: arthropods in a grassland (open circles) and those in a potato field (solid circles). For further explanation see text.

where the values of constants were obtained from $\lambda=13.7$ and $C=5450 \text{ cm}^2$ (cf. KOBAYASHI, 1974, p.234).

The equation (5) is applicable also to the data taken by the use of utterly discrete sampling unit. Fig.5B shows fitness of the equation (5) to the data of arthropods collected by sweeping in a grassland (MOTOMURA, 1935) and those counted on potato plants (KOBAYASHI, unpublished) (cf. Fig.2 of KOBAYASHI, 1974). As the size of sampling unit was a pool of 20 sweeps in the former and one plant in the latter, x was temporarily assumed to be $100n$. The fitted equations are as follows :

Arthropods in grassland : $S=22.3 \log (1+x/41.7)$,

Arthropods in potato field : $S=7.6 \log (1+x/17.8)$.

The values of constants in these equations were found by the same method as given in p.267. Their characteristic area, $C=71.7$ for the arthropods in grassland and $C=30.6$ for those in potato field, indicates that if the size of sampling unit reduces to 71.7 per cent (viz., a pool of 14.3 sweeps) in the former and to 30.6 per cent in the latter, the equation (10) will hold in both data.

DISCUSSION

The sampling unit has hitherto been defined in different ways in addition to area. As for animal communities, the number of individuals or the time of trapping was more general than area. Using this measurement of sample size, WILLIAMS (1943) has developed his law of collection enrichment that doubling the number of insects caught (and hence the time of trapping) at any level, except for very small sample, always adds approximately constant number of species to the total. This implies that the number of species in collection increases linearly with the logarithm of the time of collecting. MOTOMURA (1935) has already described this law using the sweeping record of arthropods, and has pointed out that it was restatement of ROMELL's (1925) equation.

ROMELL's (1925) or GLEASON's (1922) equation for the species-area relation was

$$S=b+a \log x \quad (13)$$

where a and b are constants. If we let n be equal to infinity the equation (11) approaches to the equation (13) which has $a=2.3v$ and $b=u+v\gamma$, because

$$\lim_{n \rightarrow \infty} \{ \Sigma(1/n) - \ln n \} = \gamma$$

where γ is EULER's constant. The equation (5) or (6) approaches to the equation (13) for larger area because 1 is negligible compared with x/E or $\rho x/\alpha$ as suggested by WILLIAMS (1943) and HOPKINS (1955).

Applicability of the equation (13) for larger area has fully been demonstrated by EVANS *et al.* (1955). They showed that the total number of vascular plant species present in an area of 54,000 square yards can satisfactorily be predicted from a set of square yard samples placed at random in the area.

Another idea that the species-area relation is not logarithmic but parabolic has

been put forward (ARRHENIUS, 1921 ; PRESTON, 1960 and 1962 ; KILBURN, 1963 and 1966). According to this idea, the fitted equation is

$$S = kx^z \quad (14)$$

where k and z are constants. KILBURN (1966) has pointed out, however, that in most cases actual plots for larger area fall below the parabola. The equation (14) is probably an approximation for smaller area.

The other maintenance that the species-area curve is sigmoid may still be worth examining. In his first paper, PRESTON (1948) has suggested that WILLIAMS's law of collection enrichment is an approximation of the integrated curve of lognormal. This is nothing but an acceptance of the sigmoid species—log area curve. Similarly, BRIAN (1953) has proposed an alternative equation for the relation between the number of species (S) and that of individuals (ρx) in area x based on the negative binomial series :

$$S = T\{1 - (1 + \rho x/kT)^{-k}\} \quad (15)$$

where T denotes the limit of S as x increases and k a constant reflecting species richness. This equation also shows a sigmoid curve.

A simpler model for an imaginary condition that the individuals of each species are distributed at random with the same abundance has been proposed by KYLIN (1926): His equation was

$$S = T(1 - e^{-m\alpha}) \quad (16)$$

where m is the number of individuals per unit area per species and T the same as in the equation (15). This equation is the form obtained by putting k to infinity in the equation (15).

An essential difference of the sigmoid curve from others may be the existence of asymptote or the delimitation of universe. Although GOODALL (1952) said that this argument carries little weight since the area is also limited, it may be a matter for argument whether the number of species increases steadily or retards to increase as the area expands logarithmically. In this regard, HAIRSTON (1959) has suggested that owing to the strong clumping of rare species, with increased sampling new rare species are more likely to be added to the total than are additional specimens of rare species already recorded. The contagiousness in the spatial distribution of rare species may thus prevent the species-log area curve being sigmoid.

SHINOZAKI (1959) has considered that in the case where a community of homogeneous pattern expands so largely that the flora or fauna is exhausted, the sigmoid species-log area curve (the closed type in his term) will be observed. According to him, if survey is ceased at intermediate area within a closed type community, the parabolic or logarithmic curve (the open type) will be obtained. This might imply that most of the species-log area curves become sigmoid if sufficiently large area is surveyed. However, if a habitat is prevented from immigrating or invading by the species whose populations are originally centered in other habitats, the closed type

community will be found. In view of the community continuum (see CURTIS, 1955; WHITTAKER, 1952 and 1956) it may be reasonable to regard our data as a fragment of the continuum, so that the chance of encountering newcomers will never be exhausted even in fully large area. Perhaps this is acceptable explanation for the open type curve, and may be supported by the fact that some of the closed type species-log area curve ceases to be sigmoid when sampling area expands further (ARCHIBALD, 1949b; HOPKINS, 1955).

There is another matter to be noted. The uniformity of specific density may be in favor of the suggestion that homogeneous habitats are nearly saturated with species (MACARTHUR, 1965). According to the present model, once the values of λ and E are assigned, the number of species can be predicted by area. On the other hand, in remote islands which have not been saturated with species because of the difficulties in immigrating or invading, the number of species is likely to be regulated by other factors than area (HAMILTON *et al.*, 1963). In so far as homogeneous and unisolated habitat is concerned, therefore, the equation (5) may reflect the capacity of habitat for sustaining species at a given area.

The area is somewhat different measure from other importance value of species such as the number of individuals, biomass and productivity. It should be noticed that in the species-area relation the criterion is merely presence or absence of species. For this reason we may get a consistent result, whereas the species-abundance relation is of varied forms and lacks neatness as suggested by WHITTAKER (1965). Further investigation on the relative abundance of species is necessary.

SUMMARY

A second mathematical model describing the species-area relation was proposed for continuous expanding of sample area. This model is expressed as

$$S = \lambda \ln(1 + x/E)$$

where S is the number of species occurring in an area x , and λ and E are the constants termed *specific diversity* and *elemental area* respectively. As a result of testing the validity of the model for several sets of data, it was shown that the above equation would provide an adequate fit to a group of species belonging to a single synusia which exists in an open habitat.

The ecological implications of parameters involved were discussed and the characteristic area presented previously (KOBAYASHI, 1974) was defined in terms of E . The relation between results obtained by discrete sampling and continuous sampling was examined and the possibility of converting one to another was suggested.

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種数・面積関係 II. 連続サンプリングの場合のモデル

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前報 (KOBAYASHI, 1974) に続いて、サンプル面積を連続的に拡大した場合に出現する種数を記載するモデルを提案した。面積 x に出現する種数を S としたとき、モデルは

$$S = \lambda \ln(1 + x/E)$$

で表わされ、 λ と E は常数で、それぞれ種多様度 (specific diversity) および要素面積 (elemental area) と呼ぶ。このモデルの妥当性をいくつかのデータを用いて検討した結果、上式は、ある λ と E の値によって特徴づけられる種のグループ、すなわち、ひとつの *synusia* に適用されるべきものであって、2以上の *synusia* を含む群集に対しては、異なる λ と E の値をもつ複数の上式が混合されていると仮定した場合、実測データとの良い一致が認められた。

上式に含まれるパラメーター λ と E の生態学的意義を吟味し、前報で提案した特性面積 (characteristic area) を E に基づいて定義した。また、不連続サンプリングの場合のモデルと連続サンプリングの場合のモデルの関係を論じ、ある条件下では両者が相互に変換可能であることを示唆した。