THE SPECIES-AREA RELATION FOR ARCHIPELAGO BIOTAS: ISLANDS AS SAMPLES FROM A SPECIES POOL

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INTRODUCTION

In earlier stages, the mathematical description of species-area relation for samples drawn from a universe provoked much discussion among phytosociologists (see Goodall, 1952; Greig-Smith, 1964). Although no sound conclusion has been attained, some ecologists have been in favor of the view that the number of species (S) found in an area (x) is described by a power function

\[ S = Kx^z \]

where \( K \) and \( z \) are constants (e.g. Preston, 1962; Kilburn, 1966; Usher, 1979). Recent studies have focused on remote islands and have often shown the satisfactory fit of Eq. (1) to the observation (e.g. Preston, 1962; Hamilton et al., 1964; Hamilton and Armstrong, 1965; Johnson et al., 1968; Diamond, 1969, 1974). However, the power function has still been considered an empirical rule because of the absence of theoretical bases (Connor and McCoy, 1979).

A notable difference between the data on mainland biotas and those on archipelago biotas is that the former is collected in samples drawn from a continuous and homogeneous area, while the latter is collected from separate islands of an archipelago. This difference led to assume that the archipelago data are concerned with isolated universes (Preston, 1962). If account is taken of the immigration of species from a mainland or among islands, however, each island of an archipelago may also be regarded as a sample from a species pool.

The objectives of this paper are to reconsider the species-area relation for archipelago biotas from the viewpoint of a sampling phenomenon and to interpret the result on the basis of two models proposed before (Kobayashi, 1975, 1976).

SPECIES-AREA RELATIONS FOR MAINLAND BIOTAS

In most of the mainland data, the various sizes of sample are made up by combining the appropriate number of quadrats of a small size (Greig-Smith, 1964). Therefore, if the number of distinct species found in every combination of a given number of quadrats is plotted against the total area of quadrats combined (i.e. the product of the quadrat size and the number of quadrats combined), the plots scatter
within a range unless every quadrat has the same species composition. HOPKINS (1955) and KILBURN (1966) found that this variation in the number of species is generally small.

Figure 1 shows two typical examples obtained from the data on dipterous insects collected in grassland (KOBAYASHI, 1982) and non-predatory mites in soil (HAIRSTON, 1969). The former data consisted of 20 quadrats each collected by 10 sweeps of an insect net, and the latter consisted of 64 blocks of turf of 6.45 cm². The mean number of species, \( E(S_q) \), found in \( q \) quadrats is estimated by

\[
E(S_q) = \frac{\sum_{i=1}^{S} 1 - \binom{Q - F_i}{Q}}{q}
\]

where \( Q \) is the total number of quadrats, \( S \) is the number of species occurring in \( Q \) quadrats, and \( F_i \) is the number of quadrats in which \( i \)th species occurs (SHINOZAKI, 1963). The values of \( E(S_q) \) for the dipterons and the mites are denoted by open circles in Fig. 1.

**Species-Area Relations for Archipelago Biotas**

Suppose that each island of an archipelago can be regarded as a sample drawn from a universe (i.e. a species pool). If these islands are similar in their environmental conditions, the species-area relation resulted from the combinations of the different numbers of islands must be similar to those for the mainland biotas.

Figures 2 and 3 show the results of the following data:

(i) Mammals found on 16 islands of the Ryukyu Islands situated between Japan and Formosa (*Mayailurus iriomotensis* is added to the data of UCHIDA, 1963).

(ii) Cerambycid beetles collected on 8 islands of the Izu Islands situated south

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![Fig. 1](image_url)  
**Fig. 1.** Species-area relations for the dipterous insects (A) and the non-predatory mites (B). The solid and the open circles show the numbers of species occurring in different numbers of quadrats and the mean numbers of species occurring in a sample size, respectively. The sample size is measured in sweeps of an insect net (A) or cm² (B). The solid lines are \( S = 16.1 \ln (1 + x/13) \) in A and \( S = 33 [1 - (1 + x/10)^{-0.27}] \) in B. The broken lines are \( S = 3.54x^{0.49} \) in A and \( S = 4.11x^{0.21} \) in B.
off central Japan (data from Umeya, 1961).

(iii) Landbirds breeding on 16 islands of the California Islands situated along the coastline of southern California (data from Power, 1972).

(iv) Landbirds breeding on 15 islands of the Galapagos Islands situated about 1000 km off the coast of Ecuador (species numbers are taken from Harris, 1973, and island areas from Johnson and Raven, 1973).

(v) Seabirds breeding on 10 islands of the northwestern Hawaiian Islands (French Frigate Shoals) (data from Amerson, 1975).

(vi) Landbirds found on 52 small islands in Burntside Lake in northeastern Minnesota (data from Rusterholz and Howe, 1979).

Since the number of possible combinations of the islands belonging to an archipelago becomes too large to be treated as the number of islands increases, the plotting in Figs. 2 and 3 has been simplified as follows: From among Q islands

![Species-area relations for the mammals of the Ryukyu Islands (A), the cerambycid beetles on the Izu Islands (B), the landbirds on the California Islands (C), and the landbirds on the Galapagos Islands (D). The solid and the open circles show the numbers of species found when two or more islands are combined and those found on the individual islands, respectively. Areas are measured in km² except for C (mi²). The solid lines are $S = 50 [1 - (1 + x/115)^{-4.12}]$ in A, $S = 25.7 \ln (1 + x/50)$ in B, $S = 140 [1 - (1 + x/2.3)^{-0.97}]$ in C, and $S = 30 [1 - (1 + x/0.81)^{-0.16}]$ in D. The broken lines are $S = 0.27x^{0.54}$ in A, $S = 1.60x^{0.56}$ in B, $S = 7.46x^{0.498}$ in C, and $S = 7.19x^{0.138}$ in D.](image)
Fig. 3. Species-area relations for the seabirds on the Hawaiian Islands (A) and the
landbirds on small islands in a Minnesota lake (B). Areas are measured in ha.
The solid lines are \( S=29 \cdot \left(1-(1+x/0.6)^{-0.58}\right) \) in A and \( S=93 \cdot \left(1-(1+x/3.3)^{-0.22}\right) \)
in B. The broken lines are \( S=7.75x^{0.056} \) in A and \( S=7.00x^{0.446} \) in B. For other
symbols see Fig. 2.

of an archipelago which were numbered in sequence from the smallest to the largest,
\( q(=2, 3, \ldots, Q) \) islands with successive numbers were taken \( Q-q+1 \) times without
duplication. Then, the number of distinct species for each of these \( Q(Q-1)/2 \)
combinations was plotted against the corresponding total area of islands.

The variation of the number of species in an area is small in the Izu Islands,
while it is large in the California Islands where 4 islands of about 1 \( \text{mi}^2 \) (Anacapa,
Santa Barbara, Los Coronados, and Todos Santos) have disproportionately rich flora
and two islands of large area (Guadalupe and Cedros) have markedly poor flora.
POWER (1972) showed that the number of bird species in this archipelago is highly
correlated with the number of plant species as well as with the island area.
Although the range of variation in the number of species thus depends on the
difference of environmental conditions in each island, the scatter pattern of these
plots does not differ essentially between Figs. 1 and either 2 or 3.

**Power Function and Its Slope Value**

When Eq. (1) is applied to the mainland data, the agreement with the values
of \( E(S_0) \) is generally good as shown in Fig. 1, but it has been noticed that the
discrepancy between the observed and the calculated values increases with the
increasing area (ARRHENIUS, 1921; KILBURN, 1966). Since the number of species
occurring in a habitat is finite, the species-area curve must retard to increase in
larger areas. A single equation of power function was found to be insufficient for
Table 1. Characteristics of the species-area relations for mainland data. $x_M$ = the geometric mean of sample sizes used for obtaining a species-area relation, $S_F$ = the number of species found in all quadrats, $z'$ = the slope value of a power function, $z'$ = the slope value of Eq. (3) or (4) in a log-log plot. $\lambda$, $E$, $T$, and $A$ are the parameters of Eq. (3) or (4), and $D = x_M / E$.

<table>
<thead>
<tr>
<th>Biotas</th>
<th>$x_M$</th>
<th>$S_F$</th>
<th>$\lambda$</th>
<th>$E$</th>
<th>$T$</th>
<th>$A$</th>
<th>$D$</th>
<th>$z'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dipterons in grassland$^1$</td>
<td>67.09</td>
<td>45</td>
<td>16.1</td>
<td>13.00</td>
<td></td>
<td></td>
<td>5.16</td>
<td>0.489</td>
</tr>
<tr>
<td>Mites in soil$^2$</td>
<td>51.60</td>
<td>25</td>
<td>10.2</td>
<td>10.00</td>
<td>33</td>
<td>0.37</td>
<td>5.16</td>
<td>0.321</td>
</tr>
<tr>
<td>Insects on potatoes$^3$</td>
<td>5.67</td>
<td>14</td>
<td>7.5</td>
<td>0.18</td>
<td></td>
<td></td>
<td></td>
<td>31.84</td>
</tr>
<tr>
<td>Beetles on a lake shore$^4$</td>
<td>1.13</td>
<td>28</td>
<td>23.4</td>
<td>0.50</td>
<td>30</td>
<td>1.52</td>
<td>2.26</td>
<td>0.286</td>
</tr>
<tr>
<td>Plants in a prairie$^5$</td>
<td>3.80</td>
<td>49</td>
<td>13.7</td>
<td>0.32</td>
<td></td>
<td></td>
<td></td>
<td>11.87</td>
</tr>
<tr>
<td>Herbs in an evergreen forest$^6$</td>
<td>0.83</td>
<td>34</td>
<td>7.6</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
<td>33.22</td>
</tr>
</tbody>
</table>

Area is measured in: 1) sweeps, 2) cm$^2$, 3) plants, and 4) m$^2$.


The slope values ($z'$) of Eq. (1) fitted to six mainland data including the dipterons and the mites are given in Table 1. The data other than those shown in Fig. 1 are: insects found on 13 potato plants (KOBAYASHI, 1976), carabid and staphylidin beetles collected on a lake shore (KONTKANEN, 1957, Community II), plants found in a tallgrass prairie, and herbs found in an evergreen oak forest (RICE and KELTING, 1955). These data are confined to those consisting of a synusia or a taxocene for the reason which will be shown later. It may be notable that the $z'$ values for these data are not far from the typical ones for archipelago biotas. Other examples of the range of the $z'$ values are: 0.26—0.43 (KILBURN, 1966), 0.10—0.29 (calculated from the data of ARCHIBALD, 1949), and 0.05—0.31 (calculated from the data of HOPKINS, 1955). Thus the $z'$ values for mainland biotas fall within a narrow range which is near or somewhat below that observed in archipelago biotas.

For the six archipelago biotas shown in Figs. 2 and 3, the $z'$ values are calculated both from the data on the individual islands of each archipelago and from the data plus the total number of species ($S_F$) found on an archipelago. The results are given in Table 2.

APPLICATION OF THE ALTERNATIVE MODELS

KOBAYASHI (1975, 1976) proposed two mathematical models of the species-area relation for a single synusia or a taxocene. They were

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

(3)

if a study area is open to its surroundings, and

$$S = T[1-(1+x/E)^{-\lambda}]$$

(4)

if a study area is closed to immigration from its surroundings, where $\lambda$ is the
Table 2. Characteristics of the species-area relations for archipelago data. $x_M$ = the geometric mean of island areas of an archipelago, $hE$ = the area where one species occurs on an average. Figures in parentheses show $z$ values calculated for the data on individual islands plus the total number of species found on an archipelago ($S_T$). For other symbols see Table 1.

<table>
<thead>
<tr>
<th>Faunas</th>
<th>$x_M$</th>
<th>$S_T$</th>
<th>$\lambda$</th>
<th>$E$</th>
<th>$T$</th>
<th>$A$</th>
<th>$D$</th>
<th>$z$</th>
<th>$z'$</th>
<th>$hE$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammals on Ryukyu Isls. $^1$</td>
<td>88.26</td>
<td>18</td>
<td>6.1</td>
<td>115.00</td>
<td>50</td>
<td>0.13</td>
<td>0.77</td>
<td>0.541(0.523)</td>
<td>0.735</td>
<td>19.34</td>
</tr>
<tr>
<td>Cerambycids on Izu Isls. $^1$</td>
<td>19.91</td>
<td>50</td>
<td>26.7</td>
<td>50.00</td>
<td>—</td>
<td>—</td>
<td>0.40</td>
<td>0.562(0.601)</td>
<td>0.850</td>
<td>1.91</td>
</tr>
<tr>
<td>Landbirds on California Isls. $^2$</td>
<td>7.27</td>
<td>45</td>
<td>9.5</td>
<td>2.30</td>
<td>140</td>
<td>0.07</td>
<td>3.16</td>
<td>0.209(0.229)</td>
<td>0.507</td>
<td>0.25</td>
</tr>
<tr>
<td>Landbirds on Galapagos Isls. $^3$</td>
<td>75.85</td>
<td>23</td>
<td>4.4</td>
<td>0.81</td>
<td>30</td>
<td>0.16</td>
<td>93.64</td>
<td>0.138(0.135)</td>
<td>0.148</td>
<td>0.19</td>
</tr>
<tr>
<td>Seabirds on Hawaiian Isls. $^3$</td>
<td>0.57</td>
<td>25</td>
<td>12.8</td>
<td>0.60</td>
<td>29</td>
<td>0.58</td>
<td>0.95</td>
<td>0.566(0.532)</td>
<td>0.597</td>
<td>0.04</td>
</tr>
<tr>
<td>Landbirds in a Minnesota lake$^3$</td>
<td>1.25</td>
<td>53</td>
<td>18.4</td>
<td>3.30</td>
<td>93</td>
<td>0.22</td>
<td>0.38</td>
<td>0.446(0.438)</td>
<td>0.826</td>
<td>0.17</td>
</tr>
</tbody>
</table>

Area is measured in: 1) km$^2$, 2) mi$^2$, and 3) ha.
number of species occurring in an area of \((e-1)E\), \(T\) is the total number of species present in a habitat under study, and \(A=\ln \left(\frac{T}{(T-\lambda)}\right)\) (for the ecological meaning of these parameters, see Kobayashi, 1979a).

Eq. (3) or (4) shows close agreement with each of the average species-area relations for the mainland data (Fig. 1). The parameter values of these fitted equations are given in Table 1. When a collection comprises two or more synusiae or taxocenes, the observed species-area relation is expressed by the sum of two or more equations each fitted to a single synusia or a taxocene (Kobayashi, 1975). Therefore, the data exemplified in this paper are confined to those consisting of a single synusia or a taxocene.

For the archipelago data, since the average number of species occurring in an area cannot be determined, Eq. (3) or (4) is fitted by eye by drawing a curve passing through the point given by the total number of species found on an archipelago \(S_T\). Eq. (4) seems to be suitable for most of the archipelago data because archipelagos are isolated in varying degrees from their species pool. The species-area relations shown in Figs. 2 and 3, except for the cerambycid beetles on the Izu Islands, are therefore examined for the fitness of Eq. (4) with \(T\) values estimated as follows:

(i) The mammals on the Ryukyu Islands. Okada et al. (1965) listed 48 species certainly breeding and 8 species possibly breeding on the Kyushu Island (the nearest mainland). Then, \(T\) is estimated at 50.

(ii) The cerambycid beetles on the Izu Islands. Nakane et al. (1973) listed some 370 species which have been collected from central Japan. Since the size of the species pool \((T=370)\) is so larger than \(S_T (=50)\) that the number of species increases almost infinitely with the increase of island area, Eq. (3) is applied to the data.


(iv) The landbirds on the Galapagos Islands. About 30 landbird species are counted from the species list given by Harris (1973). Then, \(T\) is estimated at 30.

(v) The seabirds on the Hawaiian Islands. Amerson (1975) listed 29 species which have been found on French Frigate Shoals and Pearl and Hermes Reef.

(vi) The landbirds in a Minnesota lake. Rusterholz and Howe (1979) showed that 93 species breed in forested habitats in the study area.

The fitted curves are shown in Figs. 2 and 3, and the parameter values of these curves are given in Table 2. It may again be seen that the average species-area relations can be described by Eq. (3) or (4).

**The Slope Value of the Average Species-Area Relation in a Log-Log Plot**

The transformation of both sides of Eqs. (3) and (4) into logarithms gives
\[
\ln S = \ln \lambda + \ln \left[ \ln(1 + x/E) \right] \\
\text{and} \quad \ln S = \ln T + \ln \left[ 1 - (1 + x/E)^{-A} \right],
\]

which shows that when \(\ln(S/\lambda)\) or \(\ln(S/T)\) is plotted against \(\ln(x/E)\), Eq. (5) results in the same curve regardless of the values of \(\lambda\) and \(E\), while Eq. (6) results in curves which depend on the value of \(A\) alone (Fig. 4A). Denoting \(D = x/E\), we have the slope value \(z'\) in a log-log plot by

\[
z' = d \frac{(\ln S)}{d(\ln x)} = \frac{D}{\left[ (1 + D) \ln(1 + D) \right]}
\]

for Eq. (5), and

\[
z' = AD \left( 1 + D \right)^{-1 - (1 + A) / \left[ 1 - (1 + D)^{-A} \right]}
\]

for Eq. (6). Thus \(z'\) of Eq. (7) depends on \(D\) alone, while \(z'\) of Eq. (8) depends on \(A\) and \(D\). Hence \(z'\) is not constant and varies continuously from 1 to 0 with \(D\) (and therefore with area). The relation between \(D\) and \(z'\) is shown in Fig. 4B. Connor and McCoy (1979) showed that \(z\) of Eq. (1) falls within a range between 0.1 and 0.5 in most of the data they examined. Figure 4B shows that \(z'\) also falls within a similar range for a wide range of variation in the value of \(D\).

![Fig. 4. A: Curves obtained by log-log plotting of Eqs. (3) and (4). B: Relationship between \(D\) and \(z'\).](image)

If \(x\) is replaced by the geometric mean \(x_M\) of quadrat sizes or island areas (the geometric mean is used in view of the logarithmic property of species-area relation), then \(z'\) calculated by Eq. (7) or (8) with \(D = x_M/E\) may reflect the slope of the species-area relation. The values of \(z'\) thus obtained for the mainland data are close to \(z\) of Eq. (1) (Table 1), while those for the archipelago data are larger than \(z\) when \(S_T < T\) (Table 2).
THE NUMBERS OF SPECIES OCCURRING ON A LARGE ISLAND AND ON SEVERAL SMALLER ISLANDS OF EQUIVALENT TOTAL AREA

Simberloff and Abele (1976) demonstrated that the number of species found on a single island became larger when the island was turned into several smaller islands; they explained this change in terms of a power function. Higgs and Usher (1980) also reached a similar conclusion. If the number of species occurring on a single island is smaller than that on several smaller islands of equivalent total area, \( z \) becomes smaller than \( z' \). Gilpin and Diamond (1980) showed that when the number of bird species found on every pairing of 13 New Hebrides islands is related to the corresponding total area for each pair, the species-area curve in a log-log plot has a slightly larger slope value than that obtained for the individual islands. This agrees with the results shown in Figs. 2 and 3.

On the other hand, Cole (1981) asserted that a large single island will hold more species than several smaller islands of equivalent total area, although he did not present any empirical data.

Let \( p_i \) be the occurrence probability of \( i \)th species on an island of an area \( x \) and \( p'_i \) be that on \( q \) islands each having an area \( x/q \). If the \( i \)th species has a spatially uniform distribution with the population density \( \rho_i \), then

\[
\begin{align*}
    p_i &= \rho_i x & (\rho_i x < 1) \\
    &= 1 & (\rho_i x \geq 1), \\
\text{and} \\
    p'_i &= 1 - (1 - \rho_i x/q)^q & (\rho_i x < q) \\
    &= 1 & (\rho_i x \geq q).
\end{align*}
\]

That is, \( p_i = p'_i \) if \( \rho_i x \geq q \) and \( p_i > p'_i \) if \( \rho_i x < q \). Then, denoting the expected number of species occurring on the island of the area \( x \) by \( S_1 \) and that on the \( q \) islands each having the area \( x/q \) by \( S_2 \) [cf. Eq. (11)], we have the relation \( S_1 \geq S_2 \) unless \( \rho_i \) of every species is equal to or larger than \( q/x \). This is consistent with Cole (1981).

If the \( i \)th species is spatially distributed at random, then

\[
\begin{align*}
    p_i &= 1 - \exp (-\rho_i x), \\
    &\text{and} \\
    p'_i &= 1 - \left[ \exp \left(-\rho_i x/q\right) \right]^q \\
    &= 1 - \exp (-\rho_i x).
\end{align*}
\]

This implies that \( S_1 = S_2 \) if every species is spatially distributed at random.

Supposing that the individuals of the \( i \)th species are contagiously distributed and its spatial distribution can adequately be described by a negative binomial with an exponent \( k_i \), then

\[
    p_i = 1 - (1 + \rho_i x/k_i)^{-k_i},
\]

(10)
and  
\[ p'_i = 1 - \frac{1}{[1 + \rho x/q k_i]^{k_i}} \]  
\[ = 1 - \frac{1}{1 + \rho x/q k_i}^{q k_i}. \]

This implies that the difference between \( p_i \) and \( p'_i \) is equivalent to a \( q \)-fold increase of the exponent \( k_i \) (i.e. a decrease of contagiousness). Thus, if each species is distributed contagiously, \( p'_i \) is consistently larger than \( p_i \) (Table 3). However, when each species is spatially distributed in clumps, the value of \( k_i \) changes with an increase of the island area. MORISITA (1959) suggested that if the sizes of these clumps are small, the spatial distribution gradually approaches the random one as the size of sampling quadrats increases; while if the clump sizes are large, the spatial distribution remains contagious or becomes more contagious as the quadrat size increases up to magnitude comparable to the clump sizes, then it becomes random as the quadrat size increases further. It follows from this that \( S_1 < S_2 \) unless the clump sizes are very small. This is consistent with SIMBERLOFF and ABELE (1976). Since most of the organisms show the spatially contagious distribution, it may generally be observed that the number of species on one large island is less than that on several smaller islands of equivalent total area, and therefore \( z < z' \). KOBAYASHI (1983) has illustrated the species-area curves of the dipterons and the mites for the various values of \( k_i \).

**DISCUSSION**

The species-area relation for island biotas has so far been interpreted in several ways. They were brought under three categories: habitat-diversity hypothesis, area-per-se hypothesis, and passive-sampling hypothesis (CONNOR and McCoy, 1979).

The environmental factors such as elevation, topographic complexity, and the intensity of human impact may affect the species richness on an island. However, since the scatter patterns of the species-area plots for the archipelago data are virtually the same as those for the mainland data which have been collected each in a homogeneous habitat, one cannot ascribe the positive correlation between species

<table>
<thead>
<tr>
<th>No. of islands ((q))</th>
<th>Area of island ((x/q))</th>
<th>Uniform</th>
<th>Random</th>
<th>Negative binomial</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>k=1.0</td>
<td>0.5</td>
</tr>
<tr>
<td>1</td>
<td>10</td>
<td>0.500</td>
<td>0.393</td>
<td>0.333</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>0.437</td>
<td>0.393</td>
<td>0.360</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>0.410</td>
<td>0.393</td>
<td>0.379</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>0.401</td>
<td>0.393</td>
<td>0.386</td>
</tr>
</tbody>
</table>
number and area to the difference of environmental diversity although it may be responsible for the range of variation in the number of species in an area.

The second interpretation, area-per se hypothesis, comprehends two principal ideas. First the canonical lognormal hypothesis has been proposed by Preston (1962) and reinforced by May (1975). This hypothesis led to a power function with $z=0.262$ as a mathematical expression of species-area relation. Its basic idea is the lognormal distribution of abundance among the species constituting a community and has been justified in terms of the central limit theorem by MacArthur (1969) and May (1975). However, the former proceeded from the dubious premise that the species constituting a community live quite independently of one another, although it might be true of such a random assemblage of organisms as a light-trap collection of moths, and the latter did not distinguish the abundances of different species in a community from those of separate and independent populations of a single species as Pie Lou (1975, p. 48) has noted. The canonical lognormal hypothesis postulates also that each island is an isolated universe, not a sample. This may be satisfied only when islands are scattered at great distances from one another. Pie Lou (1975) and Sugihara (1980) have put forward another argument that leads to a lognormal distribution of abundance. This argument, however, is based on the following biologically uncertain premises: (i) Each species joins sequentially, not instantaneously, in a community. (ii) A newcomer has an interspecific relationship to only one of the former occupants. (iii) The species to which a newly-joined species has an interspecific relationship is determined at random.

Another area-per se hypothesis is the immigration-extinction equilibrium hypothesis which has been proposed by MacArthur and Wilson (1967) and found favor with many ecologists. With this hypothesis, Schoener (1976) suggested a quadratic equation of species number as an alternative expression of species-area relation. He showed that the slope value in a log-log plot falls between 0 and 0.5. The form of his curve resembles those shown in Fig. 4A.

The interpretation proposed in this paper is based on the occurrence probability of species in an area, hence it may be comprehended in the passive-sampling hypothesis. The premises from which Eq. (3) has been derived are as follows: (i) The number of individuals (without distinction of species) is proportional to the area. (ii) The number of species occurring in an area is given by the sum of the occurrence probabilities of every species comprised in a community. (iii) More than one species cannot occur together in a very small area. (iv) A limit area where two or more species cannot occur together is determined by the biology of species comprised in a community. (v) In the extreme of very small area, the rate of increase in the number of species with an increase of area approaches the probability that an individual occurs. In addition to these five items, Eq. (4) postulates that (vi) the rate of encountering new species depends on the number of species which have not
been encountered yet (KOBAYASHI, 1976, 1979a). The second item can explicitly be described as follows: Let $p_i$ be the probability that $i$th species occurs in an area, and $X_i$ be the probability variable which equals 1 if the $i$th species occurs and 0 if it is absent, then the expected number of species, $E(S)$, found in this area is given by

$$E(S) = \sum_i p_i X_i = \sum_i p_i.$$  \hspace{1cm} (11)

Although $p_i$ depends on a number of environmental factors, it is principally determined by area. For example, if the individuals of the $i$th species are spatially distributed at random, $p_i$ is given by Eq. (9), while if the spatial distribution conforms to a negative binomial, $p_i$ is given by Eq. (10). This shows that the area is the prime predictor of $E(S)$. Thus the present interpretation views the species-area relation as a sampling phenomenon but involves biological assumptions.

To compare the goodness of fit between a power function and other models such as Eqs. (3) and (4), one should examine an observation which covers a wide range of island areas. For example, DIAMOND and MAYR (1976) found that the species-area relation for the birds on the Solomon Archipelago fits an exponential function, not a power function, as area varies over a million-fold range of magnitude. Although they considered that this is ascribable to the vagility of species, it is also possible to consider that the species-area relation fits Eq. (3) because this archipelago is open to immigration from its species pool. On the other hand, when an archipelago is largely distant from a mainland, as in the case of the birds on the Galapagos Islands, the immigration of species is almost confined within the archipelago, hence the species pool is virtually equivalent to the whole biota of the archipelago. Then, the species-area curve becomes flat as the island area increases, and it markedly deviates in form from a power function.

As Figs. 2 and 3 show, the species-area relation for archipelago biotas can be described by Eq. (3) or (4) when two or more islands are combined so as to give larger samples, while the species-area relation for the individual islands is slightly modified and approaches a power function in form owing to the spatially clumped distribution of each species. Similar modification of the species-area curves for mainland biotas has been noted when the spatial distribution of each species is contagious (HOPKINS, 1955; KOBAYASHI, 1979b, 1980).

These results lead to the conclusion that the species-area data on archipelago biotas are equivalent to the case where separate samples of different sizes are drawn from a universe in which each species is spatially distributed in clumps. This conclusion supports the suggestion that for the purpose of wildlife conservation, several smaller reserves have the advantage of holding more species than one large reserve whose area is equivalent to the total of the smaller reserves (SIMBERLOFF and ABELE, 1976; HIGGS and USHER, 1980) if these smaller reserves are open to
immigration. The specific area \((hE)\) defined as an area where one species occurs on an average (Kobayashi, 1975, 1976) suggests a critical minimum area of reserves below which the population size of a species becomes so small that it goes extinct. Putting \(S=1\) in Eq. (3) or (4), we have \(x = hE\). These values calculated for the archipelago data are shown in Table 2.

The properties of archipelago biotas which have so far been evidenced or predicted are consistent with the present interpretation as follows:

(i) Eqs. (7) and (8) show that the slope of species-area curve in a log-log plot is independent of the size of species pool expressed as \(T\) in Eq. (4). This has been predicted by Connor and McCoy (1979).

(ii) As noted previously, the species-area relation can be described by Eq. (3) if a study area is open to its surroundings, while it can be described by Eq. (4) if a study area is isolated from its surroundings. Since archipelagos are more or less isolated from their species pool, the species-area relation may mostly fit Eq. (4). On the other hand, the species-area relation for an archipelago near a mainland approaches Eq. (3). Then, as Fig. 4B suggests, the slope value becomes smaller for distant archipelagos than for near ones. This relation has been observed by Hamilton and Armstrong (1963), Schoener (1976), and Connor and McCoy (1979).

(iii) If an archipelago is near a mainland, the distance between islands of the archipelago may have little effect on the species-area relation because immigration is predominant between the archipelago and the mainland. On the other hand, the species-area relation for a distant archipelago depends on the distance between islands: The islands of an archipelago that is clumped tightly favor intra-archipelago immigration, which in turn makes the inter-island distribution of species ubiquitous. Then, since the species-area curve rises steeply toward the size of its species pool \((T)\), the value of \(A\) in Eq. (4) increases. On the contrary, for an archipelago scattered sporadically, each species is confined to a few islands because of a barrier to inter-island immigration. The species-area curve then rises slowly toward \(T\), and the value of \(A\) decreases. Thus, even if the average island area is much the same, the slope value becomes smaller for a clumped archipelago (with a large \(A\)) than for a sporadic one (with a small \(A\)) as shown in Fig. 4B. This tendency has been predicted by MacArthur and Wilson (1967, pp.29-30) on the basis of their equilibrium theory. Diamond and Mayr (1976) suggested that the species-area curve for a fauna which consists of vagile species should decrease in slope. This may also be explainable in terms of the value of \(A\).

(iv) Schoener (1976) and Rusterholz and Howe (1979) pointed out that an archipelago including large islands shows a smaller value of \(z\). Since the mean area of islands \((x_w)\) becomes large for such an archipelago, the slope value decreases as Fig. 4B shows.
MacArthur and Wilson (1967, pp. 30-32) suggested that a rapid turnover of species is responsible for the tendency that the number of species on extremely small islands does not increase with area. Figures 2 and 3 show that Eqs. (3) and (4) can explain this tendency without assuming any special condition.

(vi) The relationship between the population density \( (\rho) \) and the occurrence probability \( (p) \) given by Eq. (9) or (10) is consistent with the tendency that abundant species occur ubiquitously, while less abundant species are confined to a few islands.

(vii) Figure 4B shows that, besides the mean area of islands, \( E \) is an important parameter which determines the slope value. If other conditions are equal, the value of \( z' \) must be larger for a biota with a large \( E \) (such as mammals) than for one with a small \( E \) (such as birds). In general, areas inhabited by the species of a taxocene under study are patchily scattered within an island. Therefore, the \( E \) value obtained from the species-area data on an archipelago biota becomes larger than that obtained from the data on a single habitat because the former includes areas that are irrelevant to these species. For example, if the species-area data on the cerambycid beetles are collected in quadrats of a small size placed in a forest-edge, the \( E \) value may be so small as to be measured in \( m^2 \) or a (cf. \( E=50 \text{ km}^2 \) in Table 2). Note that the \( E \) values shown in Table 1 are measured in the magnitude of \( \text{cm}^2 \) or \( m^2 \), while those shown in Table 2 are measured in the magnitude of \( \text{km}^2 \) or ha. Since the \( E \) value thus changes with the magnitude of area, the values of \( x_M \) and \( E \) are roughly of the same order. Consequently, the dimensionless value of \( D (=x_M/E) \) falls within a range, whether the species-area data are collected in quadrats or islands. As a result, the slope value centers around 0.3 or so (see Fig. 4B). For most of the archipelago data given in Table 2, however, the \( E \) value is larger than the corresponding \( x_M \) value, which in turn results in the small value of \( D \) and a large value of \( z' \).

**Summary**

If the immigration of species from a mainland or among islands is taken into account, each island of an archipelago can be regarded as a sample from a species pool. When two or more islands are combined so as to give larger samples, the resultant species-area relation does not differ from that observed in a continuous and homogeneous habitat on a mainland. This relation can be described by either of the two mathematical models proposed before (Kobayashi, 1975, 1976). A power function seems to be insufficient because the discrepancy between the observed and the calculated values becomes larger with the increasing area. In a log-log plot, the slope values for these alternatives to a power function vary continuously from 1 to 0 as the area increases. Owing to the spatially clumped distribution of each species, the number of species found on a single island is less than that found on several
smaller islands of equivalent total area. Hence the species-area relation for individual islands has a smaller slope value than that obtained by combining the different numbers of islands and approaches a power function in form. From these results, it is concluded that the species-area data on archipelago biotas are equivalent to the case where separate samples of different sizes are drawn from a universe in which each species is spatially distributed in clumps. The properties of archipelago biotas which have so far been evidenced or predicted are consistent with this conclusion.

References


群島生物相の種数・面積関係
——種の源からのサンプルとしての島——

小 林 四 郎

連続した均一なハビタットで，一定サイズのコドラートを用いて調査した種数・面積関係は，あるひとつ
のユニバースから抽出したサンプルを取り扱っている。これに対して，島の種数・面積関係は相互に隔離さ
れた多くのユニバースに関係する問題と考えられている。しかし，種の源である本土からの，または島相互
間での移住を考慮すると，島もまたあるユニバースから抽出したサンプルとみなすことができる。この立場
から，ひとつの群島に属する複数の島を結合しているようなサイズのサンプルをつくり，種数・面積曲線を
描くと，均一ハビタットでコドラートを用いて得られた曲線と基本的に同じものとなり，既報の２つのモデ
ル（Kobayashi, 1975, 1976）のいずれかとよく一致した。しかし，それぞれの種が空間的に集中分布する
傾向があるため，複数の島に出現する種数よりも同面積の単一の島に出現する種数の方が小さくなる。した
がって，個々の島について得られる種数・面積曲線の形はベキ関数に近づき，傾斜もやや小さくなる。以上
の結果から，島の種数・面積関係は，それぞれの種が空間的に集中分布するユニバースからサイズの異なるサ
ンプルを別々に抽出する場合に相当する，と結論した。これは「受動的サンプリング仮説」のひとつであっ
て，これによって群島の生物相にみられるいろいろな特質が容易に説明できることを示した。