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PATTERNS OF ABUNDANCE AND THE FORM
OF THE SPECIES-AREA RELATION

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Numbers of species (S) are frequently related to area (A) by a power function (Arrhenius 1921) or by an exponential function (Gleason 1922). The relative abundances of species can frequently be described by a logarithmic-series distribution (LSD; Fisher et al. 1943), a negative-binomial distribution (NBD; Brian 1953), or a lognormal distribution (LD; Preston 1948). These familiar species-abundance distributions and species-area relations are themselves related. The exponential function can be derived from the LSD (Fisher et al. 1943), and the power function can be derived from the LD or the NBD (Preston 1962; May 1975; Engen 1974, 1977). I examine the assumptions of these derivations and ask whether the form of the species-abundance distribution is likely to determine the form of the species-area relation for islands.

The species-area relations.—For the exponential and power functions,

$$S = B + \alpha \ln A, \quad (1)$$

and

$$S = cA^z, \quad (2)$$

respectively, where B , α , c , and z are constants.

The species-abundance distributions.—Let f_n be the number of species with abundance n . For the NBD,

$$E(f_n) = \alpha x^n (1 + \phi)^{-k} \Gamma(k + n) / n! \Gamma(k + 1), \quad (3)$$

where $x = \phi / (1 + \phi)$ and α , ϕ , and k are constants (Rao 1971). Fisher obtained the LSD from the NBD by excluding the zero term ($n = 0$) and letting the number of individuals sampled tend to infinity as k tends to zero. Then, for the LSD,

$$E(f_n) = \alpha x^n / n. \quad (4)$$

For the LD,

$$E(f_n) = S_0 \exp\{-[\ln(n/n_0)]^2 / 2\sigma^2\}, \quad (5)$$

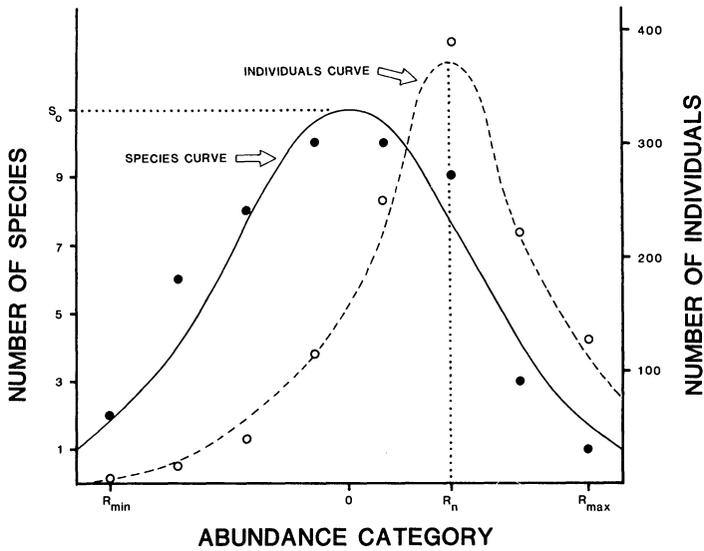


FIG. 1.—A lognormal species-abundance distribution. Abundances are scaled in logarithmic categories on the abscissa. The numbers of species in each category are plotted on the left ordinate to give the “species” curve (solid circles and solid line), and the summed abundances of the species in each category are plotted on the right ordinate to give the “individuals” curve (open circles and dashed line). The mode of the “species” curve includes S_0 species and by convention falls in category zero. The mode of the “individuals” curve falls in category R_n . Categories R_{\max} and R_{\min} include the most common and the rarest species, respectively. Data are from a Christmas count taken at Trelawney Parish, Jamaica, in 1978. Both curves were drawn by eye. Species are grouped by abundance as in figure 4.

where n_0 is the modal abundance, S_0 is the number of species with abundance n_0 , and σ is the Gaussian width of the distribution.

To derive the species-area relations, assume that the density of individuals summed over all species, ρ , is a constant and that the individuals in each community are a random sample from some larger universe. The first assumption determines the total number of individuals in each community ($N = \rho A$), and the second assumption is required to determine the expected number of species for a given N . The exponential species-area relation now follows from the LSD, and the constants α in equations (1) and (4) are equal (Fisher et al. 1943; May 1975). The power function follows from the NBD when $k < 0$ and $z = -k$ (Engen 1974, 1977).

The power function can also be derived from the LD but the second assumption must be modified. Preston (1948) grouped species' abundances into octaves, R , where each octave represents a doubling of abundance ($R = \log_2[n/n_0]$), and octaves R_{\max} and R_{\min} include the most abundant and the least abundant species, respectively (fig. 1). He then plotted the summed abundances of the species in each octave to give an “individuals” curve (Preston 1948), whose mode falls in octave R_n (fig. 1). The second assumption required to derive a species-area relation from the LD is that $\gamma = R_n/R_{\max}$ is a constant. Then, z and γ are inversely related (May 1975), and $z = 0.26$ when $\gamma = 1$ (Preston 1962).

This final result has sparked great interest. Preston (1962) first observed that $\gamma = 1$ (his canonical hypothesis) and that values of z fall close to 0.26. MacArthur and Wilson (1967) repeated this observation, and Bulmer (1974) and Sugihara (1980) developed a model of interacting populations that predicts these patterns.

Species-abundance distributions are rarely reported for islands (Haila and Järvinen 1981). The observations of Preston (1948, 1962) and MacArthur and Wilson (1967) are largely for species-abundance distributions from mainland communities and species-area relations from islands. I ask whether there is concordance between the observed species-abundance distributions and species-area relations for birds from two sample archipelagos, and I examine the assumptions outlined above.

METHODS

Censuses

Gatun Lake, Panama.—I conducted 10 1-h censuses in October 1980 and again in February and early March 1981 (unless otherwise noted) on each of the following islands: Barro Colorado (BCI, 21.5 h), Juan Gallegos, Lion Hill (17.25 h), Pantera, Puma, and Tres Almendras. I excluded migrants, nocturnal and crepuscular species, and species for which the islands were not isolated. Resident species that were excluded either commuted to the mainland to forage (vultures, parrots), foraged above or in Gatun Lake (swifts, swallows, and all aquatic species), or were poorly censused (owls, caprimulgids). I describe the study islands and give full lists of species encountered elsewhere (Wright 1979, 1985). It is important to note here that the censuses covered different portions of the six islands. BCI (1500 ha) and Juan Gallegos (670 ha) are relatively large and were subsampled. The other islands range from 7.6 to 76.5 ha and were completely censused several times.

Values of S were obtained for 14 islands in Gatun Lake in 1979. On each island, censuses were conducted until the final 20% of the cumulative census effort yielded no new species. Values of S exclude the groups listed above. Values of A were determined by planimetry from 1:25,000 scale maps (Army Map Service series E866; sheets 4243 IV SW, SE, and NE).

West Indies.—Census data come from Christmas bird counts (National Audubon Society 1973–1982) and from Lack (1976, app. 2, 4). Data from Lack were converted from his standardized numbers “seen per 10 h” to numbers actually counted. Only land birds are included because the islands are not isolated for most seabirds. The orders included are Falconiformes, Galliformes, Columbiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes. The analyses were repeated with all species from these orders and with native, resident species only. The results were qualitatively similar, and those reported here are for native, resident species only. The following censuses included too few land birds to analyze: Leinster Bay, St. John, for 1976; San Juan Bay, Puerto Rico, for 1980 and 1981; and the “strand woodland” site of Lack (1976, app. 2). Sixty-seven

censuses from nine islands remain. For the same nine islands, S was obtained from Bond (1971). Again, only native, resident land birds from the orders listed above were included.

Analyses

Species-area relations.—Linear regression was used to fit the exponential function to the species-area data, and iterative, nonlinear regression was used to fit the power function (see below). Two criteria were used to evaluate the relative fit of the two functions. First, residuals from the best-fit functions were examined. If the residuals showed no trends, the proportion of variation explained by each function was considered.

Linear least-squares regression is almost always used to fit the power function to logarithmically transformed species-area data. This procedure is correct only when error in the measurement of S increases with A . For many archipelagos, estimates of S may actually be most reliable for the largest, most frequently visited islands. Moreover, many factors that introduce error into species-area relations are unrelated to A (e.g., isolation). For these reasons, nonlinear regression should be used to fit species-area data to the power function (Wright 1981). Connor and McCoy (1979) suggested that $z \approx 0.26$ may arise as a statistical artifact of linear regression. Nonlinear-regression procedures avoid this problem.

Species-abundance distributions.—Species-abundance data were fit to the NBD and the LSD by the method of moments (Rao 1971) and to the LD by maximum likelihood (Bulmer 1974; FORTRAN program provided by R. M. Fagen, see Fagen and Goldman 1977). Estimates of maximum-likelihood parameters may be biased when the sample size (S) is small and when more than one parameter is being fit. Simulated species-abundance data were fit to the LD to evaluate this possibility. Simulated abundances were created by random draw from LD's with known parameters. Random draws were rounded to the nearest integer and values less than or equal to zero were discarded. Values of S were 20, 40, 60, 80, and 100, and the ratio of $\log n_0$ to σ equaled 2, 1.5, 1, and 0.5. Truncated lognormal species-abundance distributions occur when n_0 is small and σ is large.

Two criteria were used to evaluate the fit to observed species-abundance data. Both criteria involved deviations between observed (O) and expected (E) numbers of species, after grouping abundances such that E always exceeded five.

The first criterion considered deviations from the abundance category that included the rarest species for the LSD and the abundance category that included the commonest species for the LD and NBD. Contingency analysis was used to test the null hypothesis that negative and positive deviations were equally likely. Censuses for which $|O - E| \leq 0.5$ were not considered because O must be an integer, although E is not so constrained.

The second criterion was based on traditional χ^2 values calculated for each census. The significance of these values cannot be assessed because abundances of species are often interdependent. For example, avian censuses include accipiters and their prey, nest parasites and their hosts, and competitors. Engen (1978) suggested that χ^2 can still be calculated to form a "picture" of the fit between abundance data and a species-abundance distribution.

RESULTS

Simulated Lognormal Distributions

The simulations had two important results. First, parameter estimates matched known parameter values equally well regardless of sample size. Bias was not a problem for small samples. Second, there was a slight but consistent tendency for estimated values of σ to exceed known values for severely truncated ($\log n_0/\sigma = 0.5$) distributions. This bias emerged regardless of sample size, and its direction will prove to be important.

West Indies

The power and exponential functions explain 94% and 97% of the variation in S , respectively, and no trends are evident in the residuals from either regression model. Connor and McCoy (1979) and Wright (1981) reached the same conclusion with data sets that included 19 and 26 West Indian islands, respectively. The two regression models cannot be distinguished. For the power function, $z = 0.187$, and for the exponential function, $\alpha = 8.26$.

None of the species-abundance distributions fit the abundance data well. Censuses are not included in the following summary unless the number of abundance categories with $E > 5$ was greater than the number of parameters fit plus one. For the LSD, the NBD, and the LD, 23, 37, and 22 censuses were excluded, respectively.

Values of χ^2 exceeded conventional significance levels ($P < 0.05$) for 28 (64%), 12 (40%), and 10 (22%) of the remaining censuses for the LSD, the NBD, and the LD, respectively. Although these significance levels cannot be applied rigorously, the analysis does not suggest that the distributions describe the species-abundance data well.

Systematic deviations also occurred among censuses. For the LSD, the abundance category that includes the rarest species had fewer species than expected for 41 of the 42 censuses for which $|O - E| > 0.5$ ($\chi^2 = 38.1$, $P < 0.001$). For the NBD, the category that includes the commonest species had fewer species than expected for 15 of the 21 censuses for which $|O - E| > 0.5$ ($\chi^2 = 3.86$, $P < 0.05$). For the LD, the same category had fewer species than expected for 29 of the 35 censuses for which $|O - E| > 0.5$ ($\chi^2 = 15.1$, $P < 0.001$). There was a consistent paucity of rare species for the LSD and of common species for the NBD and the LD.

Parameter estimates for the species-abundance distributions were not consistent with parameter estimates for the species-area relations. For the parameter α of the LSD, estimated values from the species-abundance distributions were less than the estimated value from the species-area relation for 58 of the 67 censuses. For the parameter k of the NBD, estimated values from the species-abundance distributions were positive for 65 of the 67 censuses. The derivation of the power function from the NBD assumes $k < 0$ (Engen 1974, 1977).

For the LD, the relation between σ and S observed for the species-abundance data is not consistent with the slope of the species-area relation. When $z = 0.187$,

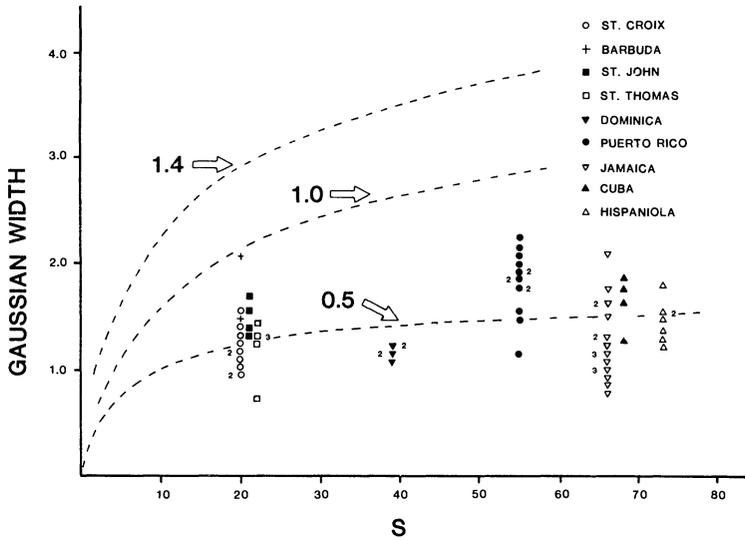


FIG. 2.—The relation between σ and S for observed and idealized species-abundance distributions. *Dashed lines*, this relation for families of lognormal species-abundance distributions for which $\gamma = 0.5, 1.0,$ and 1.4 . Symbols represent values of σ fit to observed species-abundance data by maximum likelihood; small numbers refer to multiple data sets with similar values of σ and S .

γ should equal 1.4 (May 1975). In fact, the observed relation between σ and S corresponds to $\gamma = 0.5$ (fig. 2). When $z = 0.187$, σ should fall between 3.0 and 4.0 (May 1975). In fact, the maximum-likelihood estimates for σ fell between 0.70 and 2.25 for all 67 censuses. Correcting σ for the bias found for severely truncated distributions would only accentuate the discrepancy between observed and predicted values.

Gatun Lake, Panama

The species-area relation is a power function with $z = 0.266$ ($r = 0.84$, $P < 0.01$; fig. 3). The residuals show clear trends from the exponential model. Therefore, the logarithmic-series species-abundance distribution is not considered.

The six species-abundance data sets are better described by the NBD than by the LD. Conventional significance levels of χ^2 were exceeded ($P < 0.01$) for two and six censuses for the NBD and the LD, respectively.

Despite the small number of censuses, systematic differences also occurred among censuses for the LD. There were too few common species for all six islands ($E > O + 0.5$ for the final abundance category; $P < 0.05$, binomial test), and the species-abundance distributions were not modal for the four smaller islands (fig. 4). Estimated values of k for the NBD were positive for all six censuses.

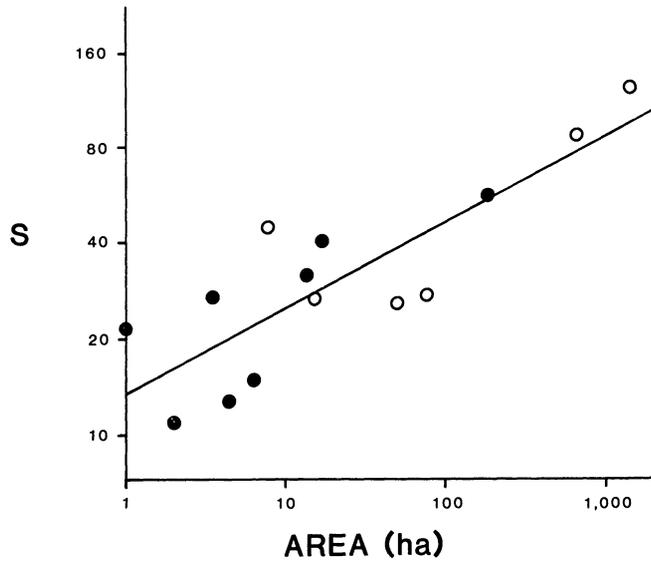


FIG. 3.—The relation between the number of species and island area for 14 islands in Gatun Lake, Panama. *Open circles*, islands for which species-abundance data are also available. The solid line was fit to a power function by iterative, nonlinear regression.

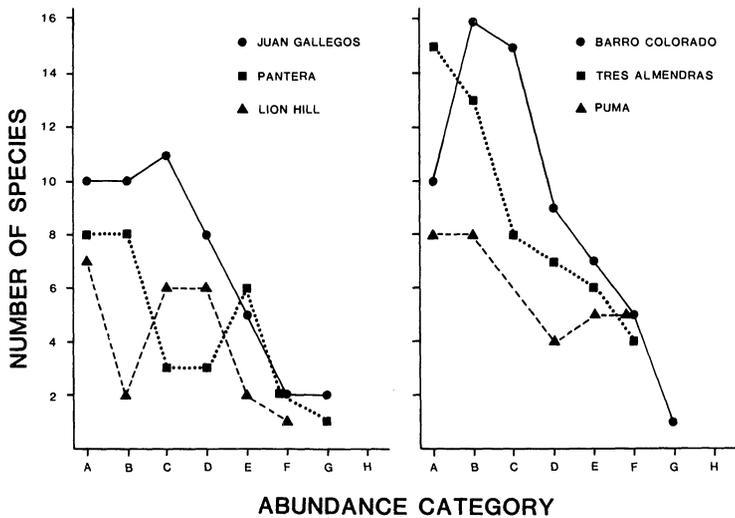


FIG. 4.—The species-abundance distributions for six islands in Gatun Lake, Panama. On the abscissa, species are grouped into categories defined by doublings in abundance. The number of species in each category is plotted on the ordinate. Category A includes species with abundance 1; category B includes abundances 2 and 3; category C, 4–7; D, 8–15; E, 16–31; F, 32–63; G, 64–127; and H, 128–255.

DISCUSSION

Derivations of species-area relations from species-abundance distributions have long been accepted (Preston 1962; MacArthur and Wilson 1967) without empirical verification (Haila and Järvinen 1981). This first attempt to examine species-abundance data and species-area relations simultaneously has not been complimentary to the theory. It remains to consider why.

When applied to islands, derivations of species-area relations from species-abundance distributions include two unrealistic assumptions. The first is that ρ , the total density of individuals summed over all species, is assumed to be a constant for all islands in an archipelago. In fact, ρ may increase, decrease, or vary independently of island area (reviewed in Wright 1980). This assumption could be relaxed by incorporating the dependence of ρ on island area. This may be a futile exercise, however, because the relation between ρ and island area appears to be an idiosyncratic property differing for every archipelago (Wright 1980).

The second problematic assumption is that the individuals on each island are a random sample from some single, larger universe. Species' abundances are affected by habitat, and it is frequently true that the larger islands in an archipelago include habitats that are not found on smaller islands. This second assumption should limit the applicability of these derivations to archipelagos where there are no systematic changes in the mix of habitats with island area.

For derivations from the LD, the second assumption is even more restrictive. First, the parameter γ must have the same value for each insular biota, and, second, the species-abundance distributions cannot be truncated. This second assumption is false for birds on islands in Gatun Lake (fig. 4) and in the Åland archipelago (Haila and Järvinen 1981). For large islands in both archipelagos, the species-abundance distributions are modal and possibly lognormal, whereas for small islands, the species-abundance distributions are distinctly non-modal and possibly truncated lognormal. The large number of very rare species found on these small islands may be maintained by frequent immigration from the nearby mainland (Haila and Järvinen 1981; Wright 1985).

The derivation based on the NBD has an additional problem. The derivation assumes that the parameter k is less than zero (Engen 1974, 1977). In fact, estimated values of k are consistently positive, as they were for 71 of the 73 censuses considered here and for 31 of 38 censuses of chironomids, collembolans, and insects reported elsewhere (Brian 1953; Engen 1974, 1978). When $k > 0$, the sums that must be computed to derive the species-area relation do not converge except when $k = 1$, when the species-area relation is linear (E. G. Leigh, pers. comm.). For this reason, the derivation of the power function from the NBD appears to be of limited biological relevance.

The LSD also has limited relevance to isolated islands. For the LSD, more species are always represented by a single individual than by any other abundance (Fisher et al. 1943). Thus, the LSD is plausible only when frequent immigration maintains small populations. Immigration rates may be sufficiently high for vagile taxa and for islands located close to a source of colonists (Lack 1969; Diamond and May 1977; Haila and Järvinen 1981; Wright 1985), but for sedentary taxa and

isolated islands, the LSD is not a biologically plausible species-abundance distribution.

The lognormal distribution remains. A consistent empirical objection to the LD is that the most common species are systematically less abundant than predicted (Brian 1953; Engen 1978; this study). The data analyzed to date are partial counts of the species in a community. Exhaustive counts of all individuals on isolated islands might produce a better fit to the LD. Such counts would include populations affected by many independent factors, and the central-limit theorem suggests that abundances might be lognormally distributed under these circumstances (MacArthur 1960; May 1975).

For this reason, the link between species-area relations and lognormal species-abundance distributions cannot be discounted at this time. The example provided by West Indian birds is not encouraging, however. Estimated values of σ were invariably smaller than predicted by the slope of the species-area relation. Avian communities from the Neotropical mainland are characterized by equally small values of σ (Preston 1980). Thus, composite counts for entire islands may produce a better fit to the LD, but parameter estimates will not necessarily be in better agreement with the slope of the species-area relation.

To summarize, theory suggests that the form of the species-area relation for islands might be determined by the form of local species-abundance distributions. I question this theory for three reasons. First, the theory is based on two assumptions that are generally false. Second, it is not clear that the appropriate species-abundance distributions are found on islands. The LSD is not sustainable on truly isolated islands, and no species-area relation has been derived for the most commonly observed NBD's. Finally, the parameters of the species-area relations and of the species-abundance distributions do not agree for the two archipelagos for which both are known. Although frequently observed species-area relations can be derived from frequently observed species-abundance distributions, this must be regarded as coincidence until species-area relations and species-abundance distributions are observed to coincide for the same archipelagos.

SUMMARY

There are several reasons for questioning whether derivations of species-area relations from species-abundance distributions apply to insular communities. First, the derivations assume that the summed density of individuals of all species is a constant. In fact, in most archipelagos this quantity varies systematically with island area (Wright 1980). Second, the appropriate species-abundance distributions may not occur on islands. The logarithmic series is characterized by large numbers of very rare species, an unlikely event when there are barriers to immigration. Derivations from the negative binomial assume that a parameter is negative, but in fact it is positive for 102 of the 111 communities that have been analyzed. The lognormal systematically overestimates the abundances of the most common species, and if species-abundance distributions observed for small islands are lognormal, they are severely truncated. Finally, the parameters of species-abundance distributions and species-area relations do not agree for birds

in the West Indies or on islands in Gatun Lake, Panama. These analyses do not suggest that species-abundance distributions determine species-area relations for insular communities.

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