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HOW DO SPECIES DIVIDE RESOURCES?

Can patterns of resource allocation be translated directly to predict patterns of species' relative abundance? Are biomass, energy, and individuals apportioned similarly among species to produce equivalent distributions each having the same variance (equitability)? Harvey and Godfray (1987) raised these fundamental questions in evaluating certain models of resource apportionment that have been proposed to explain Preston's (1962) canonical lognormal pattern of species abundance (Sugihara 1980). Canonicity here is defined by the lognormal distribution's having a specific variance (a measure of equitability; May 1975; Sugihara 1980, 1981). Harvey and Godfray concluded that if species' abundances are canonically lognormal, the biomass and energy distributions will not be canonical, although they will be lognormal. They used an allometric argument to suggest that the variances of the resource distributions will be systematically lower than the canonical variance reported for population sizes. Thus, because the apportionment of energy or biomass among species should be more equitable (lower variance) than the apportionment of individuals among species, a canonical lognormal distribution of resource use should not correspond to a canonical lognormal distribution of individuals per species, and vice versa.

This theoretical claim, although intuitively appealing, will be shown to be essentially incorrect. Moreover, the predicted lower variance of the biomass and energy distributions is not upheld by the data. Rather, the data suggest the rather surprising hypothesis that biomass, energy, and individuals may be divided among species with roughly similar patterns of equitability. The broader implication of this finding is that to a first approximation, published results of species' equitability patterns that are based on either individuals or biomass but not standardized may in fact be broadly comparable.

Harvey and Godfray's analysis begins with the observation that population density N tends to decrease with individual body weight B according to $N \propto B^{-x}$, $x \leq 1$ (see Damuth 1981; Peters 1983; Brown and Maurer 1986). This means that in the biomass distribution, the biomass per species, $B' = NB$, should follow $B' \propto N^{1-1/x}$. Assuming that the proportionality factor is a true constant, it follows that the variance of the log of species biomass B' for a community will be

$$\text{var}(\log B') = (1 - 1/x)^2 \text{var}(\log N). \quad (1)$$

Similarly, because per capita basal energy E scales with body weight, B , as $E \propto B^y$ (Damuth 1981; Peters 1983), the basal energy, $E' = NE$, consumed by a species having a population size N tends to follow $E' \propto N^{1-y/x}$ with $x \leq 2y$. Therefore, the

variance of the log of species energy consumption becomes

$$\text{var}(\log E') = (1 - y/x)^2 \text{var}(\log N). \quad (2)$$

If we accept the parameter ranges for y and x suggested by Harvey and Godfray, both $\text{var}(\log B')$ and $\text{var}(\log E')$ should be less than or equal to $\text{var}(\log N)$. That is, both the log of the species' biomass and the log of the species' energy distributions should be more equitable than the log of the species' abundance distribution.

In the above discussion, the allometric expressions for B' and E' were treated as if they had been derived from perfect regressions having no scatter about the regression lines. That is, Harvey and Godfray assumed that deviations about the expected values given by the regression equations have no effect on the total variance of the biomass and energy distributions. It can be shown that this assumption is not justified and, more specifically, that this additional source of variation contributes to the total variance in the following manner:

$$\text{var}(\log B') = (1 - 1/x)^2 \text{var}(\log N) + 1/x^2 \text{var}(\epsilon_1) \quad (3)$$

and

$$\text{var}(\log E') = y^2/x^2 \text{var}(\epsilon_1) - \text{var}(\epsilon_2) + (1 - y/x)^2 \text{var}(\log N), \quad (4)$$

where ϵ_1 and ϵ_2 are the errors (deviation from the expected values) for the regression of $\log N$ on $\log B$ and $\log E$ on $\log B$, respectively. Thus, the variance of the log of the biomass per species predicted by equation (1) underestimates the true variance, whereas the relative variance of the log of energy use per species depends on the specific magnitudes of the regression errors involved. Therefore, it is difficult to use equations (1) and (2) to predict whether biomass, energy, or individuals should be more equitably distributed among species.

To illustrate how ignoring the regression errors in equations (1) and (2) can produce misleading estimates, I shall compare Harvey and Godfray's allometric estimate with an actual value measured from real data for a community (fig. 1; Holmes and Sturges 1975). Here, the estimated value for the standard deviation of $\log B'$ is computed by fitting x to the data on $\log N$ versus $\log B$ for this community and plugging this value into equation (1). The value obtained by this method is 6.60. This compares poorly with the actual value of 1.09 computed directly from the data.

This more complete picture suggests that it is not possible to make unequivocal statements about the relative magnitudes of these variances from simple allometric arguments. Yet, the insightful question that Harvey and Godfray raised concerning how these quantities are apportioned remains of fundamental interest. To investigate this, instead of presenting a theoretical argument, I compute $\text{var}(\log B')$, $\text{var}(\log E')$, and $\text{var}(\log N)$ directly from published data on a variety of natural assemblages and compare them (see figs. 1, 2). Each point of figure 1 represents a different natural assemblage chosen arbitrarily to span the various major taxa originally fit to the canonical lognormal distribution. The data in figure 2 are more difficult to come by and represent samples taken in three consecutive years from four different ponderosa pine bird communities (Szaro and Balda 1979). Both of these figures consider only the variance of the values as reported

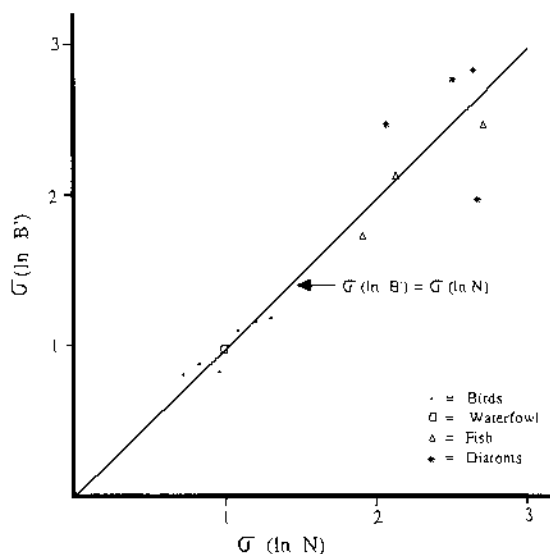


FIG. 1.—Standard deviation of the log of biomass per species versus the standard deviation of the log of population size. The data tend to cluster about the 45° line, indicating equality of variances. Sources: forest birds (Holmes and Sturges 1975; Szaro and Balda 1979); waterfowl (Poysa 1983); fish (ponds with and without young) (Swingle 1950); diatoms (variance of volume) (Beers et al. 1977, CATO, leg 1, 0 m, 20 m, 100 m, 200 m).

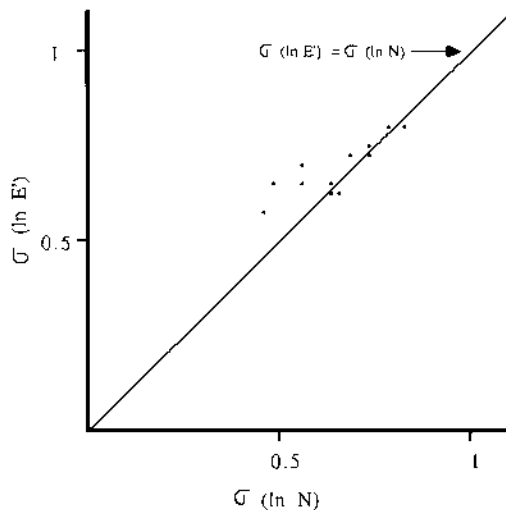


FIG. 2.—Standard deviation of the log of basal energy consumed per species versus the standard deviation of the log of population size. The clustering about the 45° line indicates equality of variances. Data on ponderosa pine bird communities from Szaro and Balda 1979.

without considering measurement error. In figure 1, biomass per species, B' , was either directly measured or computed from mean body weight. Because these mean body weights were usually determined by measuring B' directly and then dividing by N , no further error is introduced by calculating back to obtain B' . The data on energy use in figure 2, however, are more problematic, in that it is not practical to make direct measurements (e.g., by labeled water) on the energy used by each species within a community. These data, therefore, were computed by Szaro and Balda (1979) by using the five-parameter Weiner-Glowacinski relationship for passerine birds. The variance obtained by this method is not well documented. Acknowledging these potential problems, I focus this analysis operationally on the equitability of apportionment of biomass, energy, and individuals as measured and reported in published data sets. Although this is a more phenomenological question, it is nonetheless meaningful, since one would like to know the relationship, if any, between relative abundance patterns reported in the literature as biomass or energy and those reported in terms of individuals per species.

As can be seen in figure 1, the biomass distributions appear to possess essentially the same variance as the corresponding population-density distributions. This observation has been recorded briefly elsewhere (Sugihara 1983). Notice that the points fail to fall systematically below the 45° line as predicted by Harvey and Godfray. Within the range examined in figure 2, the energy distribution and the population distributions have approximately the same variance. For reasons discussed above, these data are less conclusive. Both the energy and biomass distributions may tend to be less equitable at lower variances and more equitable at higher variances; however, within the range encountered, equality of variances is not a bad approximation.

Although these results must be regarded as preliminary, they suggest the approximate empirical hypothesis

$$\text{var}(\log N) \approx \text{var}(\log B') \quad \text{and possibly} \quad \text{var}(\log N) \approx \text{var}(\log E'). \quad (5)$$

This is a curious and nonintuitive result, which must depend in part on the insensitivity of these measures. It suggests, moreover, that canonicity in population density implies canonicity in the biomass and energy distributions.

The apparent interchangeability of equitability measures supports the possible legitimacy of Harvey and Godfray's interpretation of the niche-hierarchy model of species' relative abundance (Sugihara 1980). The niche-hierarchy model was proposed to explain Preston's canonical lognormal distribution as a consequence of an underlying hierarchy in niche similarities, such as portrayed in a niche-overlap dendrogram. The metaphorical generating mechanism for this model is a sequential binary breakage process with break points reflecting the branching structure in niche similarities. In general, the breakage in this model should not be thought of as a one-time physical occurrence. Rather, it describes a dynamic constraint for how proportional abundances may fluctuate in time within a hierarchically structured system (Sugihara 1983, MS). Harvey and Godfray, however, interpreted this model literally to represent the direct allocation of resources (biomass or energy). The distribution produced thereby is a resource distribution and not an abundance distribution for the species. If their interpretation and

allometric argument are correct, this model, which produces a canonical lognormal resource distribution for the species, would not explain the canonical lognormal abundance pattern, since the variance of $\log N$ would be systematically higher. As we have seen, however, this argument (though reasonable) is not correct. Rather, because the variance of the resource-use distributions tends to approximate the variance of the species' abundance distribution, the niche-hierarchy model, even interpreted strictly as Harvey and Godfray did, remains a viable explanation of Preston's canonical hypothesis.

It should be mentioned that the observed equality of variances does not follow if species' abundances are independent of per capita resource requirements. Such independence was mistakenly suggested by Harvey and Godfray as an assumption of the niche-hierarchy model. In every case in the assemblages shown in figures 1 and 2, the population density (N) tends to decrease with increasing per capita resource use (B and E). Indeed, the equality of variances given in relationships (5) requires the following correlations among these quantities:

$$\text{cov}(\log N, \log B) \approx -\frac{1}{2} \text{var}(\log B)$$

and

$$\text{cov}(\log N, \log E) \approx -\frac{1}{2} \text{var}(\log E),$$

where again B and E are the per capita biomass and basal maintenance energy. Plainly, equality of variance implies that body weights and individual energy requirements are not independent but must co-vary negatively with population size in a manner roughly equal to half the variance of the per capita resource requirements. Thus, for relationships (5) to hold, such that canonicity applies equally to species' abundance, species' biomass, and species' energy distributions, population sizes within a community must tend to decrease as body weight and per capita energy requirements increase.

In sum, it is incorrect that resources should be apportioned among species more equitably than are population numbers. Rather, the data suggest that, to a first approximation, these quantities are distributed among species in a community with roughly similar patterns of equitability. This fact implies a curious correlation among body size, basal energy, and population size, allowing for possible interpretations of the niche-hierarchy model in terms of biomass, energy, or individuals.

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