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The meaning and measurement of size hierarchies in plant populations

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Summary. The term "size hierarchy" has been used frequently by plant population biologists but it has not been defined. Positive skewness of the size distribution, which has been used to evaluate size hierarchies, is inappropriate. We suggest that size hierarchy is equivalent to size inequality. Methods developed by economists to evaluate inequalities in wealth and income, the Lorenz curve and Gini Coefficient, provide a useful quantification of inequality and allow us to compare populations. A measure of inequality such as the Gini Coefficient will usually be more appropriate than a measure of skewness for addressing questions concerning plant population structure.

Introduction

Most plant populations exist as size hierarchies of individuals. By size hierarchy we mean a frequency distribution of individual plant sizes in which relatively few individuals contribute most of the population's biomass and most individuals are relatively small. Such size frequency distributions have been described in laboratory and greenhouse populations of plants (Yoda et al. 1963; Obeid et al. 1967; Ford 1975) and in natural field populations (Ogden 1970). Size differences may be caused either directly or through variation in growth rates by factors such as age differences, genetic variation, heterogeneity of resources, competition, or the effects of herbivores, parasites or pathogens. The ecological and evolutionary implications of size hierarchies in plant populations are enormous. There is evidence (e.g. Solbrig 1981; Werner and Caswell 1977; Sohn and Policansky 1977) that size is correlated with fitness in plants, and an inordinately large proportion of a plant population's genes may be descended from a very small number of individuals in previous generations (Leverich and Levin 1979).

Researchers have not addressed the phenomenon of size hierarchies in plant populations directly; the term "size hierarchy" is vague and has had different connotations ascribed to it by different researchers. Here we attempt to clarify the concept and provide a mathematical definition.

The definition of size hierarchy

The intuitive definition of a term, the way it is most commonly used, is the appropriate place to start if we are to make it more explicit. Unfortunately, the term hierarchy has different meanings in different disciplines, and this has contributed to confusion about its use by plant population biologists with reference to size frequency distributions. Hierarchy is defined by the Shorter Oxford English Dictionary (Third Edition) as "a body of persons or things ranked in grades, orders or classes ...". This is consistent with the concept of a size distribution, in which one ranks individuals and assigns them to successively larger size classes. We believe that size hierarchy most appropriately refers to characteristics of the size distribution, and does not, by definition, imply a hierarchy of power or exploitation. These hierarchies may also exist and may be related to size, but this must be demonstrated. As used by researchers, the term "size hierarchy" is usually applied to size distributions which have certain attributes: (1) The population contains large variation in individual sizes; (2) There are relatively few large individuals and many small ones; (3) These few large individuals contribute greatly to the population's biomass, i.e. they are dominant in the sense of vegetation science.

Beyond referring to size hierarchies loosely, several researchers have considered positive skewness of the size distribution to be the essential characteristic of a size hierarchy. Standardized measures of skewness based upon the third moment around the mean (e.g. $g_1 = n \sum_{i=1}^{n} (x_i - \bar{x})^3 / (n-1)(n-2)s^3$) (Sokal & Rohlf 1981) have been used to measure the degree hierarchy. For example, an increase in positive skewness of the size distribution with increasing plant density has been considered evidence for the hypothesis that interference results in dominance of some individuals and suppression of others (White and Harper 1970); similarly, decreasing skewness with increasing density has been considered evidence against the dominance/suppression hypothesis (Turner and Rabinowitz 1983). We believe this to be inappropriate and misleading. Positive skewness of the size frequency distribution and size hierarchy overlap little in meaning as skewness reflects only the second of the three aspects of a size hierarchy listed above. Although the degree of variation in sizes is important to the intuitive notion of a size hierarchy, measures of skewness are designed to be insensitive to the degree of variability. A population consisting of fifty individuals of size one unit and five individuals of two units is less of a size hierarchy than a population with the same number of small individuals and with five individuals of ten units, although the distributions are equally skewed (Fig. 1). Put another way, the vari-

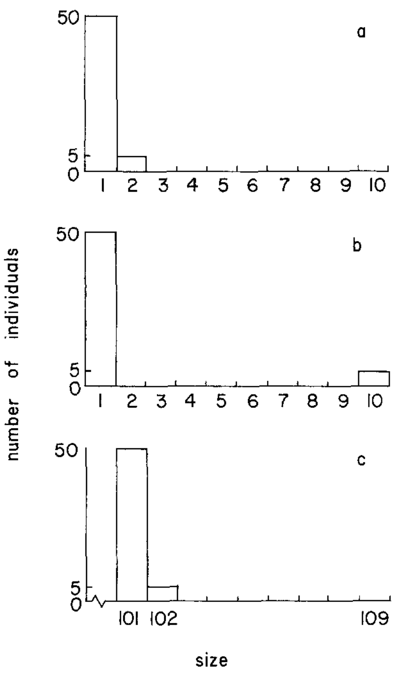

Fig. 1a–c. Three size frequency distributions which are equally skewed ($g_1 = 2.93$) but very different in their degree of hierarchy

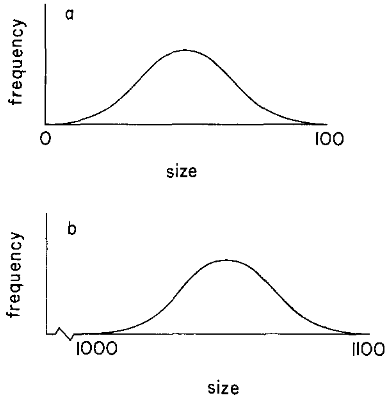

Fig. 2a, b. Two non-skewed size frequency distributions. Distribution **a** is much more hierarchical than distribution **b**

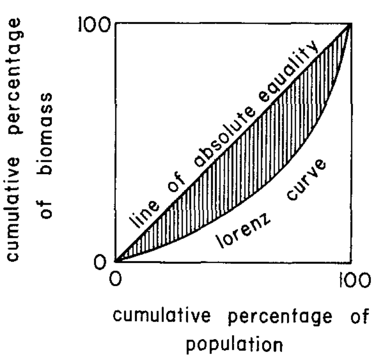

Fig. 3. The Lorenz curve as applied to size inequalities or hierarchies in plant populations. The area between the curve and the line of perfect equality expressed as a proportion of the area under the diagonal is called the Gini Coefficient and is a measure of inequality (after Sen 1973)

ation in the size of individuals relative to the mean size of an individual is important to the notion of hierarchy [components (1) and (3) above] although this is not addressed by any measure of skewness or asymmetry. For example, if the difference in size between the largest and smallest individuals in a population is only a few percent, the population would not be very hierarchical, although it may have a highly skewed size distribution (Fig. 1c). This is especially relevant for large woody perennials. An even-aged stand of large trees may show a highly skewed size frequency distribution, but this would not be of great interest if the coefficient of variation of sizes were very low. The standard practive of comparing size frequency distributions which are expressed in terms of a certain number (usually twelve or twenty) of size classes without any units for these classes (e.g. Koyama & Kira 1956; Ford 1975) obscures this very point. Finally, if sizes vary greatly relative to the mean there may be a considerable degree of hierarchy, even if the size frequency distribution is not skewed (Fig. 2a). The largest few percent of the population may still account for much of the total biomass, whereas a similar distribution with the same variance but a larger mean (Fig. 2b) would be considered less of a hierarchy.

We conclude that it is the concept of size inequality or concentration, not asymmetry, which corresponds to the notion of a size hierarchy. If all individuals are equal in size there is no size hierarchy; the degree to which biomass is concentrated among a few individuals is the degree of the size hierarchy.

Results

To find a measure of hierarchy or inequality we have looked into the literature of economics. Economists have used the Lorenz curve (Lorenz 1905; Bowman 1946) to represent graphically the degree of inequality in the distribution of wealth or income in societies. This method can be applied to size inequalities in plant populations (Fig. 3). Individuals are ranked according to biomass and the cumulative percentage of biomass is plotted against the cumulative percentage of the population. Perfect equality will result in a diagonal line from the origin to the upper right corner. While economists do not agree on what is the best measure of economic inequality because of problems in defining a relevant social welfare function (Atkinson 1970), the degree of deviation from the diagonal is a good measure of inequality. This can be evaluated as the ratio of the area between the diagonal and the curve over the triangular area under the diagonal, and is called G, the Gini Coefficient (Gini 1912; Ricci 1916). Thus, G has a minimum value of 0, when all individuals are equal, and a theoretical maximum of 1.0 in an infinite population in which all individuals but one have a value of 0: the ultimate in inequality. G is equal to one half of the relative mean difference, i.e. the arithmetic average of the absolute values of the differences between all pairs of individuals (Sen 1973):

$$G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \bar{x}}.$$

The behavior of G corresponds well to the behavior of our intuitive concept of a size hierarchy. For example, the values of G for the exemplary size frequency distributions in Fig. 1 are (a) 0.075, (b) 0.409 and (c) 0.001. The Gini

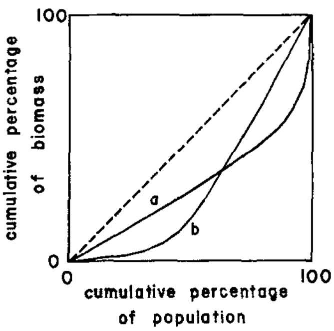

Fig. 4. Two Lorenz curves which have the same Gini Coefficient

Coefficient has many of the characteristics we would like in a measure of inequality. One of these qualities is that its value does not change if each individual's size is raised in the same proportion. Thus it is possible to compare inequalities in populations with different means, or in one population over time.

The Gini Coefficient may be thought of as the most important summary statistic for the Lorenz curve but, like any summary statistic, it does not contain all the information in the data. Different Lorenz curves can have the same value for G, e.g. curves a and b in Fig. 4. In curve 4a the inequality present is primarily due to the very few large individuals and the equality present is mostly from equality among the smaller individuals. In curve 4b the inequality is primarily from the occurrence of very small individuals, while the equality present reflects equality among the numerous larger individuals. In addition to measuring overall inequality through the Gini statistic, analysis of Lorenz curves may contribute to our understanding of plant size distributions. For example, linear portions of the Lorenz curve represent modes. Bimodality will appear as two relatively linear sections separated by a bulge, which reflects a valley in the distribution. Mathematical analysis of Lorenz curves may be useful in evaluating bimodality and other aspects of size distributions.

The calculated G for a small sample is a biased estimator of the population's G. Sample G's can be multiplied by $n/(n-1)$ to give unbiased estimates of the true population G. Obtaining error estimates for G has proven challenging because it is unclear what, if any, assumptions can be made about the underlying distribution of Gini Coefficients in the real world. Recently developed "bootstrapping" procedures (Diaconis and Efron 1983; Efron 1982) enable us to obtain error estimates for many sample statistics without assumptions by examining the statistic's distribution among numerous artificial samples created from the sample. Bootstrapping has been employed to obtain confidence intervals for Gini Coefficients of plant size distributions, and to test for significant differences between populations (Weiner MS).

Whether or not one agrees with our use of the term size hierarchy, inequality is an important aspect of plant size and reproductive distributions which has not been given attention. We propose that researchers employ the Gini Coefficient rather than measures of skewness when asking questions about plant population structure. For example, increases in size inequality with increasing density is what we should expect if plant interference results in dominance and suppression.

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