

## INEQUALITY AND DIVERSITY: INSIGHTS FROM BIOLOGY

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**ABSTRACT.** Inequality is a significant topic in economics and human society, with parallels in biology at the levels of individuals, organizations, and ecosystems. It seems, however, that the mathematics underlying these phenomena is very similar, and a new field of research, Econobiology, evolves.

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### 1. LAMÉ CURVES IN BIOLOGY AND ECONOMY

Gabriel Lamé (1795-1860) introduced the curves named after him in order to apply Descartes' beautiful geometry to the study of crystals [31]. The set of Lamé curves is very general, but of particular interest are the closed curves, also known as supercircles and superellipses. In recent years, these superellipses have been used in a number of studies to examine natural forms, and these curves can be found everywhere, from the stomata of plant leaves [33], to the shape of leafs and fruits [34, 52, 66], the growth rings of trees [51, 26, 27], and the shape of the culms of square bamboos [25]. Lamé's fingerprint is everywhere, not just in plants.

In these studies, the polar form of superellipses was used, or rather a special case of a generalization, known as Gielis formula [16, 17, 59]. This geometric transformation has been applied to the shapes of starfish [53], diatoms [14, 15], and flowers [64, 63, 57], and has been widely used in technology, among others in antennas and communication [4, 67, 68, 32], in nanophotonics [46, 45, 47], laser technology [10], and many other fields [21, 20, 3]. This generic geometric transformation can be applied in almost any direction, including in geometry [30, 35, 58] and applied mathematics [36, 7, 6]. Recently, the Gielis formula inspired the generalization of inner and vector products, and of quaternions [40, 41].

Superellipses are also widely used in economics, especially in production functions, which have recently been studied by geometers [60, 61, 8]. The Constant Elasticity of Substitution

production function which describes a relationship in which the ability to substitute one input for another (or one good for another) remains constant, regardless of the level of output or utility, is defined as:

$$(1.1) \quad Y = A [\alpha K^\rho + (1 - \alpha)L^\rho]^{1/\rho}$$

where:

- $Y$  is output,
- $K$  is capital,
- $L$  is labor,
- $A$  is a productivity parameter,
- $\alpha$  is a distribution parameter (weighting capital vs. labor),
- $\rho$  is a parameter related to the elasticity of substitution.

In the original publication [1], Arrow and co-authors showed that the Cobb-Douglas case occurs as a limiting form when capital and labor can be perfectly and proportionally substituted. When  $\rho \rightarrow 0$ , the function reduces to the Cobb-Douglas production function:

$$(1.2) \quad Y = AK^\alpha L^{1-\alpha}$$

In [1] three ways of proving this are shown, the most interesting of which is the one based on power means. In their book (*Inequalities*) [22] Hardy, Littlewood, and Polya show that as the order of the power mean converges to zero, it converges to the geometric mean. The theorem states that for positive numbers  $x_1, x_2, \dots, x_n$ , the power mean of order  $r$  is defined as:

$$(1.3) \quad M_r(x_1, x_2, \dots, x_n) = \left( \frac{1}{n} \sum_{i=1}^n x_i^r \right)^{1/r}$$

As  $r$  approaches zero,  $M_r$  converges to the geometric mean:

$$(1.4) \quad \lim_{r \rightarrow 0} M_r(x_1, x_2, \dots, x_n) = \left( \prod_{i=1}^n x_i \right)^{1/n}$$

A special case is  $r = 1$ , when the power mean reduces to the arithmetic mean, and the geometric mean. This coincides with our studies of superellipses and superparabolas, which result either from the addition, or from comparisons of  $x^n$  and  $y^m$ , ( $y^n = x^m$ , or  $y = x^{m/n}$  with the parabola  $x = y^2$ ). Power laws, which are omnipresent in nature and the sciences [5, 65, 37, 38], are superparabolas. According to the rules of arithmetic,  $x^n$  and  $y^n$  are the outermost entries in Pascal's triangle. These entries of type  $x^n y^0$  or  $x^0 y^n$  are the most unlikely outcomes that can occur when tossing a coin. But what is most unlikely is preferred by nature (Figure 1)[18].

## 2. MODELING INEQUALITY IN ECONOMICS

Inequality in the economy and in human society, manifests itself through disparities in income, in the distribution of resources and wealth, and in social structures [42, 39, 19]. The mathematical studies of inequality go back to Pareto, but especially since [42], the focus has been on the top 1 or the top 0.1 percent of income earners. However, it should be noted that this is a dynamic phenomenon. Students tend to have low incomes, but these rise over the course of their careers in industry or academia. At the end of their careers, they are usually in the top

Variables	Planar curves	Types	Special means
$x^n + y^n$	Supercircles & Superellipses	Lamé curves	Arithmetic mean $\frac{x+y}{2}$ (for $n = 1$ )
$x^n \cdot y^m$	Superparabolas & Superhyperbolas	Power laws	Square of geometric mean $\sqrt{x \cdot y}$ (for $n = m = 1$ )

FIGURE 1. Combining the most improbable of outcomes

deciles of income, but on retirement most fall back into the lower deciles. This dynamic is well documented [56, 2, 24].

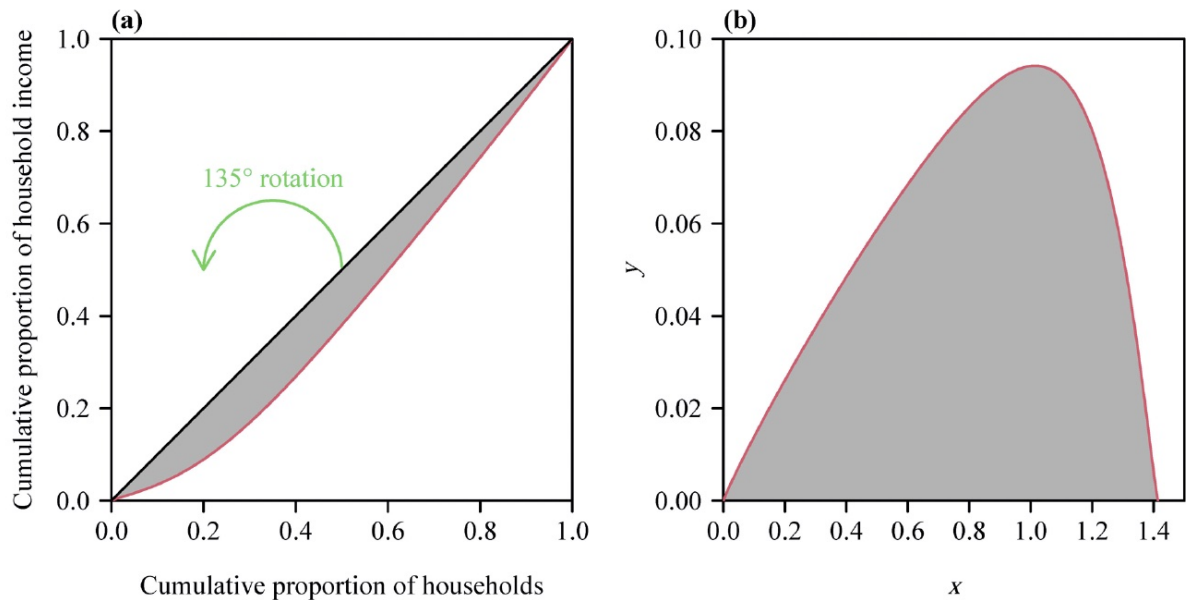


FIGURE 2. Left: Lorenz curve with cumulative proportion of households versus cumulative proportion of household incomes. Right: a  $135^\circ$  rotated and right shifted Lorenz curve [28]

The Lorenz curve graphically represents the cumulative distribution of income (Figure 2,[28]), with the Gini coefficient quantifying the area between the curve and the line of perfect equality. There are various ways to represent the Lorenz curve mathematically. *Modeling Income Distributions and Lorenz Curves* [9] provides a good overview of the various methods. Figure 3 shows examples of equality, Pareto and exponential functions, and Figure 4 shows a systematic extension of Pareto-type functions.

The Pareto type models and variations are related directly to superellipses [48]. The Lamé superellipse was used successfully as a one-parameter model for the study of inequality [23]

$$(2.1) \quad L(p) = \left(1 - (1 - p)^k\right)^{1/k}$$

Distribution	C.D.F	Lorenz curve
Equal	$F(x) = \begin{cases} 0, x < \mu \\ 1, x \geq \mu \end{cases}$	$L(p) = p$
Pareto	$F(x) = 1 - (a/x)^a, x > a, a > 1$	$1 - (1 - p)^{(a-1)/a}$
Exponential	$F(x) = 1 - e^{-\lambda x}, x > 0$	$p + (1 - p)\ln(1 - p)$

FIGURE 3. Cumulative Density Functions and corresponding Lorenz curves

Using data from 89 countries sourced from the Luxembourg Income Study, this one-parameter model fit observed income distributions efficiently [23].

Lorenz curve	Gini
$L_0(p) = L_0(p; k) = 1 - (1 - p)^k$	$G = \frac{1 - k}{1 + k}$
$L_1(p; k; \alpha) = p^\alpha [1 - (1 - p)^k]$	$G = 1 - 2[B(\alpha + 1, 1) - B(\alpha + 1, k + 1)]$
$L_2(p; k; \gamma) = [1 - (1 - p)^k]^\gamma$	$G = 1 - \frac{2}{k} \left[ B\left(\frac{1}{k}, \gamma + 1\right) \right]$
$L_3(p; k; \alpha; \gamma) = p^\alpha [1 - (1 - p)^k]^\gamma$	$G = 1 - 2 \sum_{i=0}^{\infty} \frac{\Gamma(i - \gamma)}{\Gamma(i + 1)\Gamma(-\gamma)} B(\alpha + 1, ki + 1)$

FIGURE 4. Variations on Lorenz curves of Pareto type and corresponding Gini Indices

### 3. PERFORMANCE EQUATIONS IN BIOLOGY

When considering Lorenz curves and Gini coefficients to model inequality in biology, Dr. Peijian Shi found that the curves that result when a Lorenz curve is rotated  $135^\circ$  and shifted to the right, with the starting point 0 and the end point  $\sqrt{2}$  (Figure 2, right), are very similar to the curves that represent the performance equations in biology [19]. We refer to this transformation as Shi rotation [19]. Such performance curves are very common in biology. In the original paper, the performance of frogs was studied (“how far they jump as a function of temperature” [29]), and they are also found in the development rates of insects [54, 55, 50]. They are typically modeled as product exponentials:

$$(3.1) \quad c(1 - e^{-K_1(x-x_1)})(1 - e^{K_2(x-x_2)}),$$

with  $x_1 = 0$  and  $x_2 = \sqrt{2}$  as start and endpoints, respectively. This model and some variations, for example, the generalized performance equation

$$(3.2) \quad c(1 - e^{-K_1(x-x_1)})^a(1 - e^{K_2(x-x_2)})^b$$

were tested on bamboo leaves and melon fruits [62], and on the diversity of tree size in forests [69]. In all cases, the Shi-rotated Lorenz curve agrees well with the biological data based on dynamic processes (Figure 5). The Gini indices were 0.2379 for fruits, 0.1208 for Shibataea leaves, and 0.2684 for the size of trees in a forest. The values for leaves and tree size are lower than the lowest Gini indices for inequality in Western European countries. Gini indices for Europe, South-Asia, the Middle East, Northern Africa, USA and Canada range from 0.28 (Belgium) to 0.39 (US). The Gini indices for Sub-Saharan Africa and South America are higher than 0.4 [39, 19].

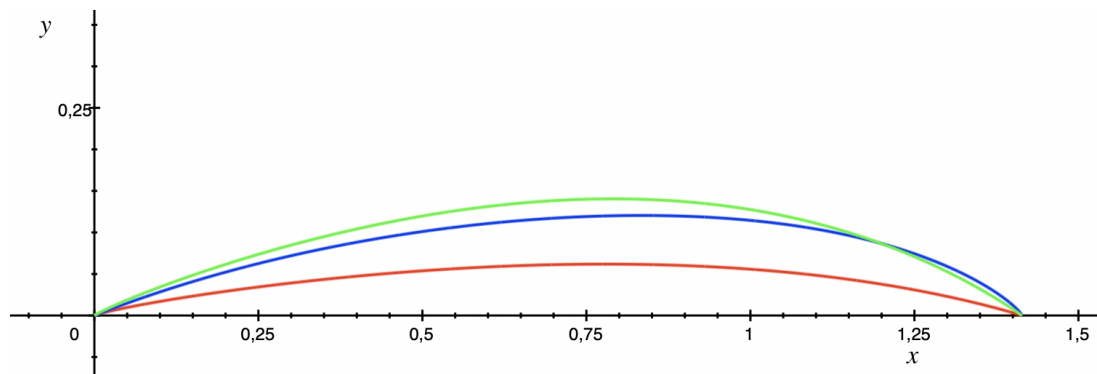


FIGURE 5. Three Lorenz-Shi curves with Equation (3.2) of the size of melon fruits (Blue)  $c = 0.2033, K_1 = 1.5335, a = 0.9958, K_2 = 2.6217, b = 0.8053$ ; Shibataea leaves (Red)  $c = 8.8721, K_1 = 0.0077, a = 0.8348, K_2 = 1.0619, b = 0.9716$ ; Tree size in forests (Green)  $c = 2.4476, K_1 = 0.1203, a = 0.9044, K_2 = 1.0915, b = 0.9739$

When comparing various other models for Lorenz curves, GPE performed better than three other Lorenz equations in terms of goodness of fit, and the trade-off between goodness of fit and structural complexity of the model [49]. GPE is a powerful tool for quantifying size distributions over a wide range of organic units and can be used in a variety of ecological and evolutionary applications. Even for the simulation data of hypothetical, extremely skewed distribution curves, GPE still performed well [49]. The Gini coefficient, a measure of *inequality* both in economy and biology (resulting from our studies), is strongly correlated with other measures of *diversity* in biology, suggesting a mathematical unity across domains. Three other measures are the coefficient of variation  $CV$  (3.3), the Theil index  $T$  (3.4) and generalized entropy index  $GPE(\alpha)$  (3.5):

$$(3.3) \quad CV = \frac{\sigma}{\mu}$$

$$(3.4) \quad T = \frac{1}{n} \sum_{i=1}^n \frac{A_i}{\mu} \ln \left( \frac{A_i}{\mu} \right)$$

$$(3.5) \quad GEI(\alpha) = \begin{cases} \frac{1}{n} \frac{1}{\alpha(\alpha-1)} \sum_{i=1}^n \left[ \left( \frac{A_i}{\mu} \right)^\alpha - 1 \right] & \alpha \neq 0, 1 \\ \frac{1}{n} \sum_{i=1}^n \frac{A_i}{\mu} \log \left( \frac{A_i}{\mu} \right) & \alpha = 1 \\ -\frac{1}{n} \sum_{i=1}^n \log \left( \frac{A_i}{\mu} \right) & \alpha = 0 \end{cases}$$

- The Gini index is proportional to the coefficient of variation (CV).
- Theil index is proportional to the square of the CV and to the square of the Gini index
- The Theil index is the generalized entropy index with  $\alpha = 1$ .
- Half of the  $CV^2$  is the generalized entropy index with  $\alpha = 2$ .

#### 4. GEOMETRIC RELATIONSHIPS

**4.1. Areas and Optimization.** Overall, Lamé curves and product exponentials establish close links between inequalities in plants and nature, and phenomena in the economy. This will provide new and powerful methods to gain insights into how nature and societies are structured and function - a new era of Eco(no)biology. Comparing the Gini coefficients of size distribution in plants with income distribution in countries, one is tempted to conclude that plants are more successful than humans in size distribution and resource allocation. The class of Generalized Conic Sections which include supercircles and superellipses, as well as superparabolas and superhyperbolas, is pure geometry. In the same way that classic conic sections are related to areas (for example the Pythagorean Theorem, Kepler' law of areas, and the parabola as a machine turning rectangles into squares with the same area), for each of the Generalized Conic Sections, specific trigonometric functions and Pythagorean conservation laws can be developed. For supercircles, Pythagorean identities have already been derived [44], and in particular the trigonometry on the diamond and the related Fourier expansions [43]. But the recent results in [40, 41] also open the door for generalizing the notion of orthogonality tailored for generalized conic sections. Such generalizations will be possible for trigonometric functions on the hyperbola and the parabola as well. In the next section an overview of the basic functions is given. In further sections two examples are given, one on the relationship between product exponentials and hyperbolic functions (section 4.3), and one on generalized logistic functions (section 4.4).

#### 4.2. Trigonometric functions and Area.

##### 4.2.1. Circular functions.

- $\cos \theta, \sin \theta$  satisfy the Pythagorean identity:  $\sin^2 \theta + \cos^2 \theta = 1$
- An angle  $\theta$  (in radians) defines a sector with area  $A = \frac{1}{2} r^2 \theta = \frac{1}{2} \theta$
- Thus,  $\theta = 2A$ , where  $A$  is the sector's area.

##### 4.2.2. Hyperbolic functions.

- $\cosh u, \sinh u$  satisfy the identity:  $\cosh^2 u - \sinh^2 u = 1$ .
- The parameter  $u$  (hyperbolic angle) corresponds to a sector from  $(1, 0)$  to  $(\cosh u, \sinh u)$ , with area  $A = \frac{u}{2}$
- Thus,  $u = 2A$ .

##### 4.2.3. Parabolic functions [13, 11].

- ${}_p c(\phi), {}_p s(\phi)$  satisfy the Parabolic-Pythagorean Identity:  ${}_p c(\phi)^2 + {}_p s(\phi)^2 = 1$ .
- The parameter  $\phi$  is defined as twice the area of the parabolic sector formed by:
  - The x-axis from  $(1, 0)$  to  $({}_p c(\phi), 0)$ ,
  - The ray from the origin to  $({}_p c(\phi), {}_p s(\phi))$ ,

- The parabolic arc from  $(1, 0)$  to  $(pc(\phi), ps(\phi))$ .
- The area  $A$  is given by:  $\frac{1}{2}pc(\phi) \cdot ps(\phi) + \int_{pc(\phi)}^1 (1 - \xi^2) d\xi = \frac{1}{2}\phi$ .
- Thus,  $\phi = 2A$ .

**4.3. Product exponentials and hyperbolic functions.** Exponential functions are directly related to conic sections, with  $e$  defined on the hyperbola for  $area = 1$ . In the simplest form, the product exponentials from biology have  $K_1$  and  $K_2$  equal to 1. Figure 6 shows curves for  $(1 - e^{-x})$  (red) and  $((1 - e^x))$  (blue) and two product exponentials (black).

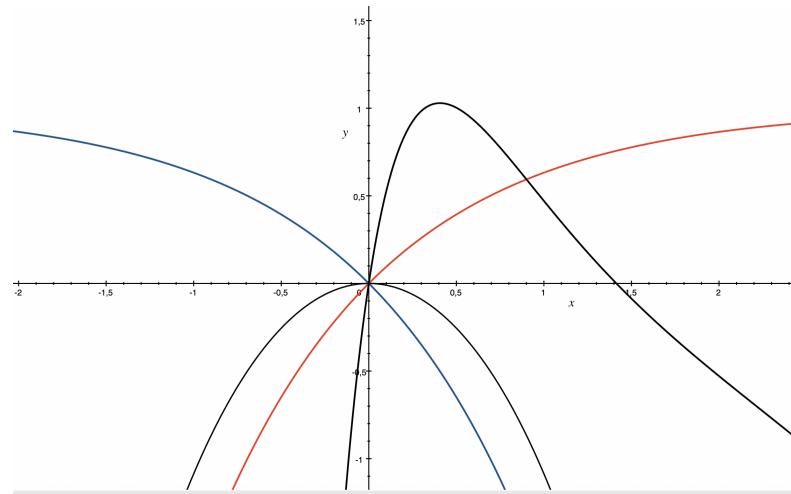


FIGURE 6. Graphs for  $(1 - e^{-x})$  (red),  $(1 - e^{+x})$  (blue), and two product exponentials (black): One is  $-4 \sinh^2\left(\frac{x}{2}\right)$ . The other product exponential is  $y = 0.4(1 - e^{+0.5x})(1 - e^{-2.5(x-1.414)})$

One of the product exponential curves is actually directly related to hyperbolic functions, in particular  $\sinh(x/2)$ . Indeed:

$$(4.1) \quad (1 - e^{-x})(1 - e^x) = -4 \sinh^2\left(\frac{x}{2}\right)$$

Further, for  $((1 - e^{-x})(1 - e^x))^n$ , the result is

$$(4.2) \quad -4^n \sinh^{2n}\left(\frac{x}{2}\right)$$

**4.4. Generalized Logistic Functions.** Performance equations are products of exponential functions of the type

$$(4.3) \quad (1 - e^{-x})$$

which are directly related to the logistic equations or logistic functions (LF). The LF belongs to the family of sigmoid curves, which are ubiquitous in all areas of science. They play a central role in the study of all non-linear evolutionary processes that exhibit growth and saturation and cover many phenomena in physics, biology, ecology, economics and population growth. Different

forms of logistic equations can be embedded in a single framework [12]. The logistic function (LF) is defined as:

$$(4.4) \quad F(x, r|K) = f_0 \frac{e^{rx}}{1 + \frac{f_0}{K}(e^{rx} - 1)}$$

This describes a growth process, counteracted by a reduction of the gain.

$$(4.5) \quad \hat{F}(x, r|K) = \frac{F}{K} = \frac{1}{1 + \mu e^{-rx}}, \text{ with } \mu = -\alpha K.$$

For  $\mu = -1$ , we obtain the form used in the performance equations.

$$(4.6) \quad \frac{K}{F} = \frac{1}{\hat{F}} = (1 - e^{-rx})$$

A generalized logistic function LF can include other functions  $P(x)$ , which is called the characteristic of the LF:

$$(4.7) \quad Z = \frac{1}{1 + \mu P(x)}$$

In this way it is possible to derive the associated differential equations. In [12] the example of  $P(x) = \cosh(x)$  is discussed.

## 5. CONCLUSION

Tree rings build on last year's rings, integrating all the influences of the current year, and preparing for the next year, all in a two-parameter model. Similarly, supercircles are a one-parameter model for inequality in the economy. Lorenz curves turn out to be closely related to performance equations in biology. These findings are good evidence that very simple relationships can be found in nature and in the human economy, based on areas of actual shapes and form, or of curves. The Gini and related indices are simply different but related methods to measure inequality and diversity, which seem to be two sides of the same coin. Optimization in nature is closely linked to the area, and this provides ample opportunities for exploration of new trigonometric and Pythagorean Identities for each shape. The Gielis Formula provides a gateway as a continuous transformations between shape and optimization.

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