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Phenotypic Plasticity for Allometric Laws of Ontogeny from Cellular Interactions

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Abstract

The method called Analytical Modular Dynamics (AMD) is presented within the context of Dynamical Energy Budget Theory (DEBT) using Finsler cost functionals. Focus is on how a Huxley/Needham allometric law can be a consequence of complicated Finsler dynamics between cell populations. The class of 2-dimensional Kropina metrics is fundamental for this. It is proved that plastic deformations of energy efficient interactions result in classical symbiosis, parasitism and competition, and remain conservative, although less energy efficient than before plastic deformation. Central to the discussion are the constant coefficient Volterra-Hamilton systems and perturbations of their associated DEBT energy functionals, via the Finsler-Gate Theorem, concerned with phenotypic deformation and heterochrony. A model of C.H. Waddington's ontogenetic canalization in the "epigenetic landscape" is presented exhibiting plastic deformation of phenotypic character space, using E. Nelson's stochastic mechanics.

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Finsler geometry, Volterra-Hamilton Systems, Stochastic Nelson Mechanics, Evolution, Ontogeny, Ecology.

1. Introduction

Typically, we consider idealized biological cell populations of n different types, including the somatic and germ line cells, each producing a chemical compound specific to its type. These compounds mediate biochemical changes in the model organism, which we suppose is undergoing progressive ontogenetic changes. This approach was developed in the 1990's to study the evolution of colonial organisms. The argument begins by consideration of evolutionary constraints on morphological diversity during development and is concerned with population numbers for the cell linages, biomass production, energy and cost, including repair and maintenance, within DEBT. One major problem considered was to determine possible mechanisms for two separately living cell populations to form an integrated colony. Our thinking was strongly influenced by the monograph of Leo Buss, The Evolution of Individuality, Princeton U. press, 1987. Mathematical descriptions were provided for community dynamics, from non-interacting populations through interacting populations to super-organisms and colonies, using stochastic and deterministic Volterra-Hamilton Systems, the mathematically rigorous foundation for Analytical Modular Dynamics (AMD).

True super-organisms are both individuals and colonies, for example: Siphonophores, eusocial insects, (Hymenoptera), and termites (Isoptera), plus a few types of mammals, but less so for Coelenterates Scleractinian corals or Octocorals. The Harvard biologist, E.O. Wilson [1] [2], used

Ergonomics to obtain the distribution of castes in an ant colony. We incorporate mathematical versions of this idea and together with the *Division of Labor Principle* of W.N. Bekemeshev, a Russian expert on invertebrate animals, they form the conceptual basis for a mathematical approach to colonial organisms,[3],[4],[6]. Both principles informed our recent work on the Mata-Atlantica rainforest of Brazil [5],[47],[51].

It is well known that the Serial Endosymbiosis Theory of Lynn Margulis explains how Eukaryotes evolved from Protozoa, while Leo Buss' theory concerns the evolution of metazoans from single cells. One result obtained with AMD methods was that the strongest form of division of labor, that is, optimality, *implies both cooperation and competition between castes, morphotypes and cell linages* [7].This holds for a restricted class of systems, namely, the classical constant coefficient second order ordinary differential equations (SODE's) called Volterra-Hamilton systems and holds for any number of cell types, [8],[9]. Furthermore, it followed that a system with three or more cell types disallows third party interactions. That is, distinct cell types i and j can't interact to influence another cell type, k, different from i and j. In addition, the system is *always unstable* in the sense that initially close trajectories diverge over time. These remarkable properties suggested we refer to such Volterra-Hamilton systems as, weakly coupled. They were the basis for our criticism of the Ancestral Commune Theory of Evolution of Carl Woese, [9], subsequently cited in journal, Nature, [45].

There is the example of *environmentally induced phenotypic plasticity* in Ambystoma salamanders, which are able to grow lungs by switching on a certain gene which permits them to begin life on land when their pond life is no longer feasible. This is a well-known example of heterochrony of the type known as, neoteny, [12]. The related case of modelling resource competition between the salamanders, Ambystoma laterale, and Ambystoma tremblayi, both living in the same watery habitat, the former a *sexual parasite* on the latter, has not yet been resolved,[8],[10].There is the complication that the all-female species, A. laterale, fertilizes its eggs, with A. tremblayi sperm, exclusively, and this is an interesting open problem.

Heterochrony, is the name given by biologists for phenotypic plasticity involving the suite of *time-sequencing changes* during ontogeny induced by external environmental influences, [10],[11],[12].[13]. It should be pointed out, that these are the predominant processes for evolutionary change within established body plans or morphologies (Bauplans). To paraphrase Prof. Leo Buss, *variants arising in clonal cell lineages within a multicellular organism have built their epigenetic programs and have stabilized those programs through competition with variants that failed to act beneficially for the whole. Changes in the timing of maturation of the germ cell lineage and of the somatic cell lineages which have access to heritable traits of those lineages, are the heterochronic processes that have dominated evolution of the flora and fauna on Earth for billions of years.*

Let us denote by N^i the population of all cells of type, i, in an individual organism, for example, a rice weevil of species, S. oryzae, or a colony of Scleractinian corals, say a member of the genus, Acropora. One uses, $x^i\ (t)$, to denote the total amount of the *selected* biochemical produced by all cells of type i, accumulating within the organism from a fixed starting time, T, up to time, t >T. These n variables are *taken to be the natural logs of the accumulated biomasses*.

Following V. Voltera (1936) assume the rate of production of x^i is proportional to, N^i. This is expressed (taking the proportionality constants all equal to one) as:

$$dx^i/dt = N^i, \qquad i=1, 2, \dots, n. \tag{1}$$

The n idealized cell populations exhibit interactions given by the differential equation system

$$dN^i/dt = G^i_{jk}\ (x, \mathrm{N})\ N^j N^k + r^i_j N^j\ +\ e^i\ (t), \tag{2}$$

There are n equations in (2). These include the classical "mass-action equations" formulated by the pioneers A. Lotka, V. Volterra, G. Gause, but here they are more general. The equations (1), (2), taken together constitute a *Spray* in the literature, [8],[19],[20]. This just means a solution trajectory starting at a fixed point go in any direction and that for any two points, close enough, there will be a unique solution trajectory from one to the other.

Biochemical exchanges are described by 3-index symbols, G^i_{jk}, n^3 in number (each index varies from 1 to n independently of the others). The growth rates matrix, r^i_j , has often been taken to be a constant times the identity matrix, however, it can have entries which are functions of x. The external (possibly noisy) environment is represented by, $e^i(t)$, and in some studies has been taken to be an environmental gradient [14],[15], [16]. We assume e=0 until section 5. Production of chemicals for life processes is energy consuming for any organism. The environment may stress the organism and it may only be able use its inherent phenotypic plasticity to a limited extent and there is only so much ATP to cover the various contingencies which arise during biological development. Therefore, there must be minimization, or at least conservation, of the cost of production. This is an expression of the Principle of Division of Labor and the Ergonomic Principle [3],[1],[2], [17] [18]. Denote this cost formally by F. It may be thought of as a function of three things:

(1) amounts $x^i(t')$ accumulated up to time t';

(2) rates of production $(dx^i/dt)(t')=N^i(t') > 0$;

(3) time t' itself.

Still, there are some basic facts about the formal cost F that need to be postulated. Namely, t-dependence is disallowed and:

(4) $F(x,dx/dt)>0$ for all vectors $dx/dt>0$ and $t>0$

(5) $F(x,c.dx/dt)=c\,F(x,dx/dt)$ for any positive constant c

(6) F(x,y) is bounded above on some *positive conical region* Σ of the 2n- dimensional phase space {x, dx/dt = y} and is therefore finite valued. Σ is a sub-bundle of the tangent bundle, [19], [20]. Thus, if $y \in \Sigma$, then $cy \in \Sigma$, given that $c > 0$. This is exactly *the positive cone condition.*

Note that (5) means that if the positive rate vector of production y = dx/dt is doubled, the positive cost (2) is also doubled. The same thing holds if the rate vector is tripled or quadrupled, etc. This will be true, at least for certain time scales and calibration levels, for molecular machinery observed in plants, animals, fungi and bacteria, [17], [18].

Note: If F is not explicitly dependent on, x, then the right-hand side of (2) is zero, so solutions are just straight lines in x-space so the *allometric law of Huxley and Needham* holds.

Remark: *The chemicals during ontogeny may be secondary compounds used in defense, but they are assumed to be in allometric proportion to total biomass produced*. Furthermore, after the requirements of repair and maintenance are satisfied, the Gross (i.e., Total) production is reduced to Net production. An important point is that equations (2) can be converted to Net Growth Equations from Gross Production Equations, as they are presented in (2) above.

It is important to know whether production processes satisfying 1-4 are *stable* or not. Here, the measure of stability, K, concerns *whole paths or trajectories*, $\gamma(t)$, given by solutions of (2). Those paths which start from a point with close x-values might remain close in the future, in which case *stability in the sense of Jacobi* holds. If this is false, production is said to be J- unstable. The importance of J-stability may be clarified by three comments:

(A) Since each of the n categories of biomass x^i is allometrically related to total biomass. That is,

$$x^i\,(t) = a^i_j \ln\,[m^j(t)]\ +\ b^i$$

for a constant matrix, a^i_j, a constant vector, b^i, with, $m^i(t)$, being accumulated biomass in some a priori specified time interval, [T, t], which may be small. If one choice of the n log biomasses gives J-stable trajectories, all of the allometrically related “surrogate” variables must also.

(B) J- Stability of production holds for a surrogate variable, if and only if, J-stability holds for m(t).

(C) *Reproductive biomass* is an n-vector, if there are n cell types in the model. Such a vector has components which are simultaneously allometrically related to total biomass for each type (i.e., are surrogates) then J-stability holds. *This ensures preservation of cell lineages during ontogeny (accept in cases of genetically programed cell death).*

Consider a fixed production trajectory, x (t), which is a solution of (2). For simplicity, take n=2. Choose *any* other trajectory close to C and check to see if it weaves from one side to the other of C. If *an*y solution trajectory does this, K>0, and J-stability holds. If there is a solution trajectory for which this weaving does not happen, then production is J-unstable. In such cases, close trajectories can diverge and never return, [21]. An example of J-unstable trajectories is the set of geodesic curves on a trumpet shaped surface (Horn of Gabriel). This surface has J-stability measure K=−1. But it is not a complete embedding in Euclidian 3-space, because the pole is at infinity. On the surface of the sphere of radius one, there is weaving back and forth of any chosen great circle through the North pole and any other one close by. These intersect at the North and South poles, over and over, and J- stability measure, K=1, [22]

2. Optimal Form of Division of Labor Principle

The mathematicians, L. Euler and J.-L. Lagrange, proved a theorem in the 19th century, asserting that in n-dimensional coordinate space the production paths, $\{x^i(t)\}$, which minimize Total Cost (the time integral of F between start time and finish time) must be solutions of the 2nd order system (1), (2) ,provided the matrix of 2nd order partials of, F^2, with respect to, $y = dx/dt$, is non-singular. The 2nd order equations, resulting from combining (1) and (2), cover their result, but are more general.

There are consequences from the Euler-Lagrange Theorem:

(i) The 3-index coefficients G must depend on N^i/N^j , if they have ANY explicit dependence on N. In other words, the G's are homogeneous of degree zero. This means that when interactions between cell types do actually depend on cell population sizes, N^i, it is only through their ratios.

(ii) There is no explicit t-dependence in the G's.

Let's now restrict our attention to the case n=2 , introducing, $x^1 = x$, and $x^2 = y$. One shows that the equations (2) can be re-expressed as

$$d^2y/\mathrm{d}x^2 \;=\; 2\{G^1\dot{x} — G^2\dot{y}\}\,/\,(\dot{x})^3\,,\quad \dot{x} \;=\; \mathrm{dx/dt}\,,\;\; \dot{y} \;=\; dy/dt \qquad (3)$$

a differential equation for the 2nd derivative of y with respect to x which describes the set of points $(x$,y) that are realized in the dynamical process (2). Put another way, it describes the point set of all occupied states (x(t),y(t)) occurring in an a priori specified time-interval.

The simplest example of (3) occurs when there is no x-dependence nor y-dependence in G^1, G^2. It follows that each G is zero and solutions of (3) are straight lines. This clearly implies the

$$H/N\ allometric\ law\text{:}\quad y = ax + b.$$

Here, x , is the logarithm of chemical biomass produced by population #1 and y is the same, but for #2.

A system of straight lines is always J- unstable. However, there is an infinite number of systems (5) which are J-stable and satisfy the Huxley/Needham Law. A far from trivial example is given below, as 3G-2.

A famous unsolved problem, in *Projective Geometry* stated by the German mathematician, David Hilbert, from his list of 23 problems made in the year 1900, can be understood in terms of allometry:

Hilbert's 4th Problem*: Characterize the cost functions F (x, dx/dt) satisfying (3), (4), which yield straight lines as the set of occupied states given by (2) above. Put another way, the 4th problem asks for all cost functions whose geometries have straight lines as the shortest distances between any two points. These geometries called projectively flat are exotic and are not Euclidean, generally, and the H/N-law holds. A related, but much easier, question is:*

Under what conditions does the allometric law follow from cost effective cellular dynamics?

The answer for dimension n with F a quadratic form (i.e., of Euclidean or Riemannian form), was given in the 1920's by H. Weyl, and in 1929, generalized to (2) above, by M. S. Knebelman, [23], [24]. The general case was solved 20 years later by L. Berwald, who also settled the 4th Problem for the case n = 2, but with (2) assumed to have its 3-index G's independent of N,[25]. These special "Berwald cost functionals" have been used to model ecology and evolution of colonial organisms, [4], [5[, [8], [9], [31], [46], [48], [52]. [53].

3. The Finsler-Gate: "Elastic" and "Plastic" Deformations

The Theorem below concerns a unique set of 8 constant-coefficient second order ordinary differential equations (SODE's), 3 of them, G^I, G^{II}, G^{III}, are geodesics, and all satisfy conservation laws. Moreover, the 3 geodesics are *elastic* deformations, (any one into any of the others), while the remaining 5 are *plastic* deformations of those three. Thus, the coordinate transformations describing the plastic deformations are not reversible.

1) (*) G^I, G^{II}, G^{III} $denote\ the\ three\ constant\ coefficient$ geodesic sprays. They are transformable, (any one into any other), via an appropriate coordinate transformation (non-singular). *They are by definition elastically deformable into each other. This means there are reversible transformations converting any of the three G's into either of the remaining two. The equivalence class of these three geodesics defines the Finsler Gate. The geodesics equations exhibiting the three interaction patterns are given below.*

2) (**) These 8 $coefficient\ arrays$, ${}^{(\alpha)}\Gamma^i_{jk,}$ are projectively equivalent to straight-line geodesics of Cartesian space. *Exactly 5 are obtained by non-reversible coordinate transformations of G^I, G^{II} and G^{III} and are plastic deformations. Together, these 5 interaction schemes form a set of forking paths, each path leading away from the Gate into descriptions using Finsler geometries.*

3) The concept of *heterochrony* must involve an *external influence* expressed as a vector field, C^i, to be understood as the external "driving force" behind a time-sequencing change. The elastic deformations (reversible coordinate changes) are separate from time-sequencing changes. Moreover, projective equivalence is time-sequencing equivalence, plus, any elastic coordinate changes. Projective change is a concept which provides a mathematical model of *heterochrony. There are two parts to it. In addition to the time change (s→p) along a production trajectory, a* transformation of substances produced *can occur. The reversible coordinate change models this conversion which takes place during ontogeny.*

Setting $r^i_j = \lambda\, \delta^i_j,\ \lambda > 0,$ we introduce the *total joint production parameter*, $s,$ and use $ds = \frac{1}{\lambda} e^{\lambda t} dt$ to change (1), (2) into

$$\frac{d^2x^i}{ds^2} + {}^{(\alpha)}\Gamma^i_{jk} \frac{dx^j}{ds}\frac{dx^k}{ds} = 0. \qquad (*)$$

Theorem (The Finsler-Gate)

(A) *There are* exactly 3 constant coefficient arrays G^I, G^{II}, G^{III} (*defining the Finsler Gate*) whose (*) solutions, $\gamma(s)$, are geodesics of one of the 3 conformally Minkowski Finsler metrics, i.e., $e^{\varphi_1}F^I(y)$, $e^{\varphi_2}F^{II}(y)$, $e^{\varphi_3}F^{III}(y)$, where $\varphi_1, \varphi_2, \varphi_3$ are certain linear functions of x^1, x^2 (adapted coordinate charts). There are no other 2-dimensional Finsler metrics yielding geodesics in (*). The three cost functionals are as follows:

(i) $F^I = \exp\{(1/\beta)[(1+\beta)\ln y^2 - \ln y^1]\}$, constant $\beta > 0$, $J^2 = (\beta+2)^2/(\beta+1) > 4$,

(ii) $F^{II} = |y^1| \exp\{\frac{y^2}{y1}\}$, $J^2 = 4$,

(iii) $F^{III} = \sqrt{[(y^1)^2 + (y^2)^2]}\exp\{L \arctan(y^1/y^2)\}$, constant $L > 0$, $J^2 = 4L^2/(1+L^2) < 4$.

The proofs may be found in the appendix of [14] or [9],[47].

Each of the *coefficient arrays which together* form the Finsler Gate, GF, yields geodesics for each of (i),(ii),(iii). These in turn are classified, up to isometry, by 2 invariants: (1) curvature condition, K = 0, and (2) the numerical value of J, the *Principle Scalar*, which varies through all the positive reals, R^+, splitting this set into 2 disjoint regions, one for each F. Note that (iii) is the only cost functional that allows the Euclidean case, L = 0. Moreover, the classical ecological interactions of competition, parasitism, and mutualism *can only be derived* from (i) via certain plastic deformations, [47].

(B) There are 5 constant coefficient arrays ${}^{(1)}\Gamma^i_{jk}, \ldots, {}^{(5)}\Gamma^i_{jk}$ each giving rise to a *conservation law.* There are uniquely associated, 5 Finsler cost functionals *of the form,* $\exp\{\varphi(x)\}F(y)$, each constant along solutions $\gamma(s)$ of its corresponding spray, as above,

$$\frac{d^2x^i}{ds^2} + {}^{(\alpha)}\Gamma^i_{jk}\frac{dx^j}{ds}\frac{dx^k}{ds} = 0. \qquad (*)$$

That is,

$$\frac{d}{ds}\left(e^{\varphi(\alpha)} . {}^{(\alpha)}F\right) = 0$$

along $\gamma(s)$. These 5 are not geodesics but they do conserve cost.

Let us now display the *3 constant (positive) coefficient geodesics that define the Finsler Gate.* For each case we adjoin the production equations $dx^i/ds = y^i$, $i \in \{1,2\}$;

$$\text{(i)} \quad dy^1/ds + \beta Q_1(y^1)^2 = 0, \quad dy^2/ds + \beta Q_2(y^2) = 0,$$

$$\text{(ii)} \quad dy^1/ds + Q_1(y^1)^2 = 0, \quad dy^2/ds - Q_2(y^1)^2 + 2Q_1 y^1 y^2 = 0,$$

(iii) $dy^1/ds + 2Q_2 y^1 y^2 + Q_1[(y^1)^2 - (y^2)^2] = 0$, $dy^2/ds + 2Q_1 y^1 y^2 + Q_2[(y^2)^2 - (y^1)^2] = 0$.

The two plastic deformation equations arising from (i) are:

(iv) $dy^1/dp = -[\beta Q_1 + \sigma_1](y^1)^2 - \sigma_2 y^1 y^2$, $dy^2/ds = -[\beta Q_2 + \sigma_2](y^2)^2 - \sigma_1 y^1 y^2$,

where β, σ_1, σ_2, are positive constants and $\varphi_1 = (\sigma_1 - Q_1)x^1 + [\sigma_2 + (1+\beta)Q_2]x^2$. Note the *time-sequencing* has changed according to the parameter change, s → p , with:

$$dp/ds = A \exp\{-\int_\gamma R(x)ds\}, \qquad R(x) = \sigma_i x^i,$$

γ(s), being a solution trajectory in x-space. Such production trajectory sets are 1-dimensional and have non-zero curvature vectors. By converting to clock time, t, via the usual formula, $dp/dt = (1/\beta)\cdot\exp\{\beta t\}$, one obtains the classical interaction schemes: competition, parasitism and mutualism by choosing the appropriate signs for the coefficients. In terms of clock time, t, there will be a linear growth rate term, βN^i , added to the right-hand sides (i = 1, i = 2) and, N^i = dx^i/dt, replaces, y^i, in both equations. For example, the competition pattern will have negative signs for each quadratic term, so that, $\sigma_i > 0$ and $\beta Q_i > 0$. It is important to realize that *this competition is special* in that there is a (linearly) stable steady-state, $N_*^i > 0$. This is in marked contrast to the principle of competitive exclusion, [8, chapter 2], which states that one or the other of the two populations will go extinct. In this special instance of competition each population has a "refuge" from the other thereby facilitating the stable steady-state.

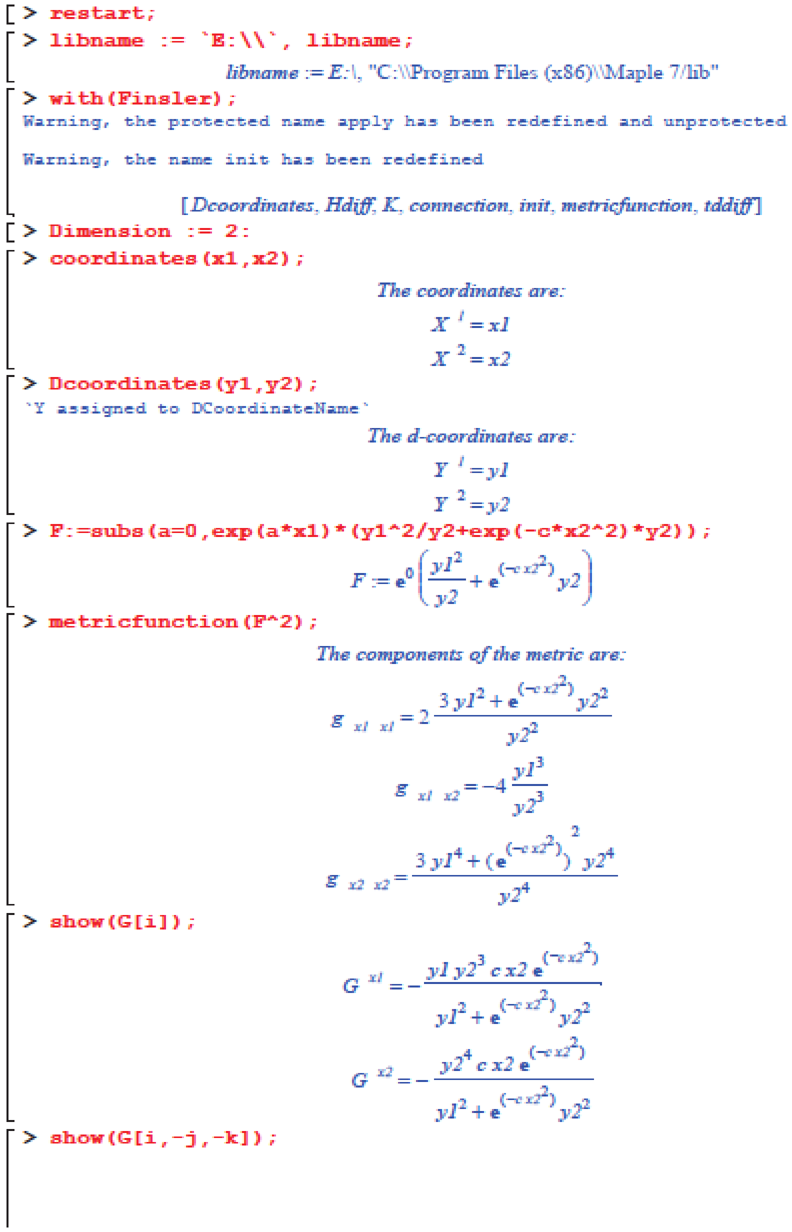
In the Master´s Thesis of Prof. S. F. Rutz' student, C. E. Hirakawa, and in [31], [46], it was recognized that evolution, via L. Margulis' serial endosymbiosis theory, eventually leads to mitochondria, yet, started as a parasitic relationship between two populations of microbes of special character. The production equations taken for the model were geodesics whose interactions were two independent logistics, as in (i) above. Its Finsler cost functional, exp $\{\varphi_1\}\cdot F^1$ had a conformal factor perturbed from a linear expression to an appropriate quadratic function of, x^i, which gave rise to x-dependent coefficients modelling Chemical Exchange and naturally interpretable as parasitic, [50]. However, that model was not (iv) above, with σ_1 and σ_2 of opposite sign, which is the classical parasite type. On the other hand, we have the Theorem: Every Constant 2- spray is Projectively Flat,[35].

This shows that production for parasitism of classical type is projectively equivalent to the double logistic, constant coefficient spray, (i). It turns out that the original model with x-dependent interactions is not projectively flat, [46], [49]. This was a great surprise largely because it contradicted statements in two published papers of M. Matsumoto and S. B$\acute{a}$cs$\acute{o}$, which quote (wrongly) a famous theorem of L. Berwald on the 2-dimensional case of Hilbert's 4th problem. A closely related Finsler cost function, was provided as formal remedy for this. Yet, the original model is still viable for modelling symbiosis in the rice weevil, S. oryzae, and its symbiont bacterium, Wolbachia, because this symbiocosm has not become highly integrated, as did mitochondria, so the H/N law would not be expected to hold.

4. Allometry: Its history and Future

The experimental work of Sir Joseph Needham, the recognized father of Chemical Embryology, [26], went beyond that of Sir Julian Huxley, [27], more concerned with morphology than with chemicals produced by vertebrate embryos during ontogenesis. Needham believed allometry was a "chemical ground plan" for development, in other words, a BAUPLAN. Today, Dr. H. Charles of Université de Lyon 1, and Dr. N. Moran of University of Texas at Austin, who research symbiont bacteria in S.oryzae and aphids, respectively, state some types of bacterial/insect symbioses obey allometric laws. However, at least one important bacterium, Wolbachia, recently involved in dengue fever research because of its disruptive effect on reproduction in its hosts, is a notable exception. It is an example of a parasitic bacterium and symbiont, which does NOT form organelles. It probably does NOT exhibit the Huxley/Needham Law, either.

It is now time for an example of a stable 2-dimensional dynamics with allometry: 3G-2 is the name given to it. The calculations were done by S. F. Rutz and her student, C. E. Hirakawa, using her software package, FINSLER, [28]. The idea used is to rewrite F(x,dy/dp) as a product, N^1 H (x, N^2/N^1), and expand H in powers of the ratio, N^2/N^1, but only up to first order approximation. This means that one or the other of the populations, but not both, must be considerably smaller than the other. There will be time intervals where this assumption holds. All such F's are called Kropina Metrics, [7],[19],[20],[29], in the literature. It has only recently been noticed that they are important in modeling ecology, development and evolution. Not a lot is known generally about this class of cost functions so that there is a wide open field for future research. It is known that (5) above for Kropina Metrics has right-hand-side a cubic polynomial in dy/dx, and coefficients depending on x and y, only, [19],[30],[31]. In fact, S. F. Rutz, her Phd student, Rinaldo, V. S., Junior and P.L. Antonelli are currently applying Finslerian Noise Theory, [14],[19], to Berwald spaces and Wagner spaces,[7], [8],[19],[20], in a problem about competition between a food crop and its transgenically modified version,[32],[33]. Wagner spaces include the class of Kropina metric spaces, for 2 dimensions.



```
> restart;
> libname := `E:\\`, libname;
```

libname := E:\, "C:\\Program Files (x86)\\Maple 7/lib"

```
> with(Finsler);
Warning, the protected name apply has been redefined and unprotected

Warning, the name init has been redefined
```

[Dcoordinates, Hdiff, K, connection, init, metricfunction, tddiff]

```
> Dimension := 2:
> coordinates(x1,x2);
```

The coordinates are:

$$X^{1} = x1$$

$$X^{2} = x2$$

```
> Dcoordinates(y1,y2);
`Y assigned to DCoordinateName`
```

The d-coordinates are:

$$Y^{1} = y1$$

$$Y^{2} = y2$$

```
> F:=subs(a=0,exp(a*x1)*(y1^2/y2+exp(-c*x2^2)*y2));
```

$$F := \mathrm{e}^{0}\left(\frac{y1^2}{y2} + \mathrm{e}^{(-c\,x2^2)}\,y2\right)$$

```
> metricfunction(F^2);
```

The components of the metric are:

$$g_{x1\ x1} = 2\,\frac{3\,y1^2 + \mathrm{e}^{(-c\,x2^2)}\,y2^2}{y2^2}$$

$$g_{x1\ x2} = -4\,\frac{y1^3}{y2^3}$$

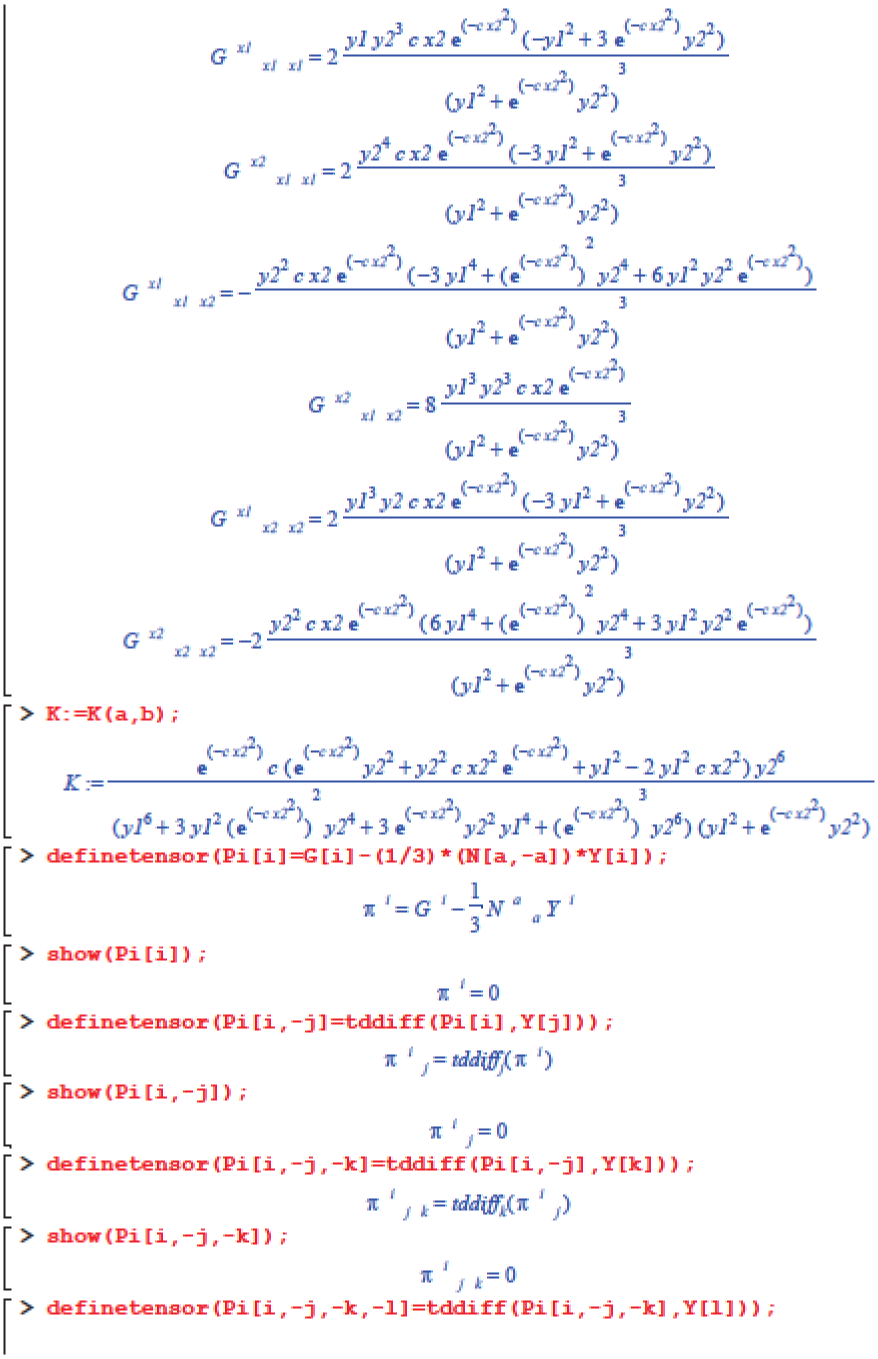
$$g_{x2\ x2} = \frac{3\,y1^4 + \left(\mathrm{e}^{(-c\,x2^2)}\right)^2 y2^4}{y2^4}$$

```
> show(G[i]);
```

$$G^{x1} = -\frac{y1\,y2^3\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}}{y1^2 + \mathrm{e}^{(-c\,x2^2)}\,y2^2}$$

$$G^{x2} = -\frac{y2^4\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}}{y1^2 + \mathrm{e}^{(-c\,x2^2)}\,y2^2}$$

```
> show(G[i,-j,-k]);
```



$$G^{x1}{}_{x1\,x1} = 2\,\frac{y1\,y2^3\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}\,(-y1^2+3\,\mathrm{e}^{(-c\,x2^2)}\,y2^2)}{(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)^3}$$

$$G^{x2}{}_{x1\,x1} = 2\,\frac{y2^4\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}\,(-3\,y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)}{(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)^3}$$

$$G^{x1}{}_{x1\,x2} = -\frac{y2^2\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}\,(-3\,y1^4+(\mathrm{e}^{(-c\,x2^2)})^2\,y2^4+6\,y1^2\,y2^2\,\mathrm{e}^{(-c\,x2^2)})}{(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)^3}$$

$$G^{x2}{}_{x1\,x2} = 8\,\frac{y1^3\,y2^3\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}}{(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)^3}$$

$$G^{x1}{}_{x2\,x2} = 2\,\frac{y1^3\,y2\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}\,(-3\,y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)}{(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)^3}$$

$$G^{x2}{}_{x2\,x2} = -2\,\frac{y2^2\,c\,x2\,\mathrm{e}^{(-c\,x2^2)}\,(6\,y1^4+(\mathrm{e}^{(-c\,x2^2)})^2\,y2^4+3\,y1^2\,y2^2\,\mathrm{e}^{(-c\,x2^2)})}{(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)^3}$$

```
> K:=K(a,b);
```

$$K := \frac{\mathrm{e}^{(-c\,x2^2)}\,c\,(\mathrm{e}^{(-c\,x2^2)}\,y2^2+y2^2\,c\,x2^2\,\mathrm{e}^{(-c\,x2^2)}+y1^2-2\,y1^2\,c\,x2^2)\,y2^6}{(y1^6+3\,y1^2\,(\mathrm{e}^{(-c\,x2^2)})^2\,y2^4+3\,\mathrm{e}^{(-c\,x2^2)}\,y2^2\,y1^4+(\mathrm{e}^{(-c\,x2^2)})^3\,y2^6)\,(y1^2+\mathrm{e}^{(-c\,x2^2)}\,y2^2)}$$

```
> definetensor(Pi[i]=G[i]-(1/3)*(N[a,-a])*Y[i]);
```

$$\pi^{i} = G^{i} - \frac{1}{3} N^{a}{}_{a}\, Y^{i}$$

```
> show(Pi[i]);
```

$$\pi^{i} = 0$$

```
> definetensor(Pi[i,-j]=tddiff(Pi[i],Y[j]));
```

$$\pi^{i}{}_{j} = tddiff_{j}(\pi^{i})$$

```
> show(Pi[i,-j]);
```

$$\pi^{i}{}_{j} = 0$$

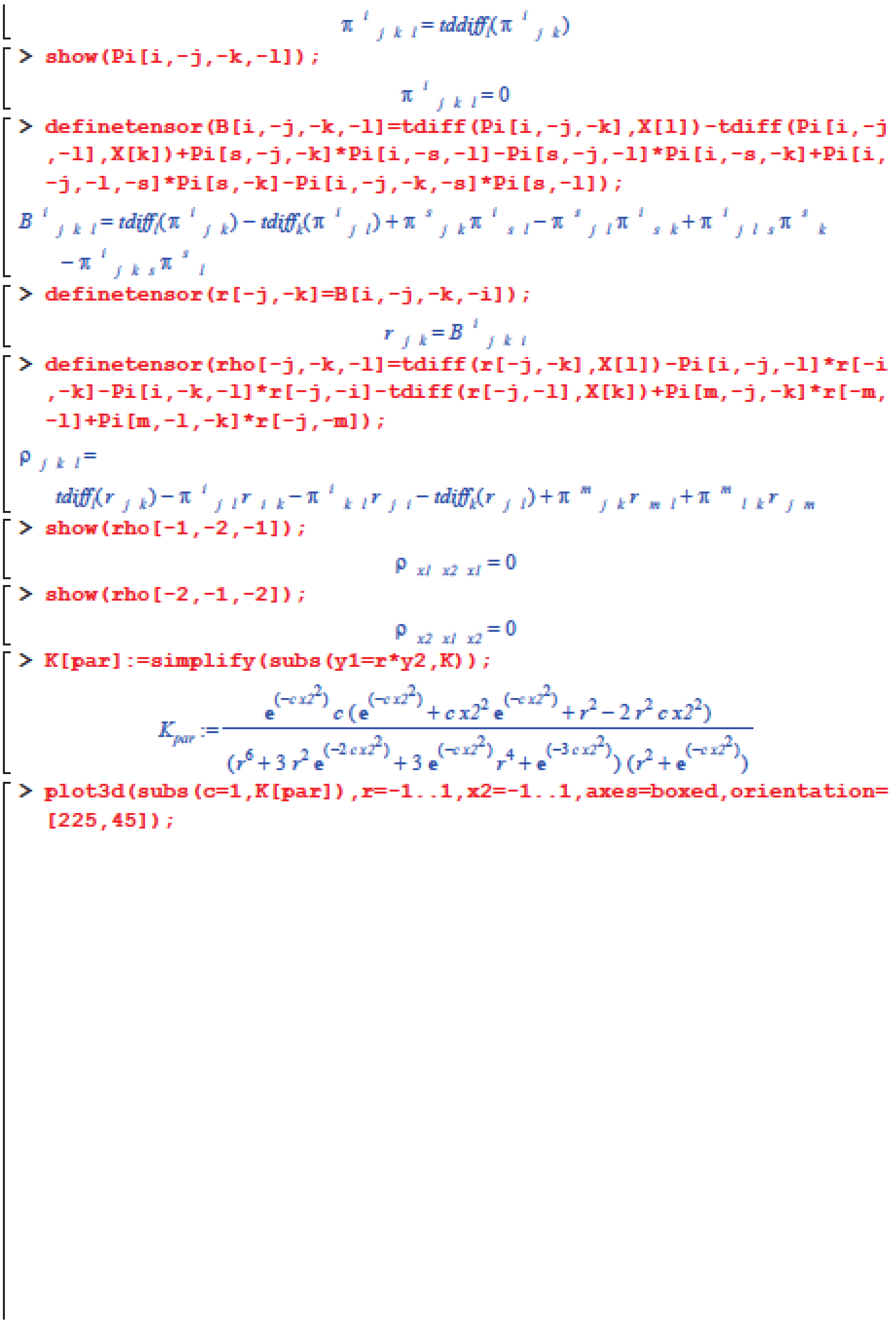
```
> definetensor(Pi[i,-j,-k]=tddiff(Pi[i,-j],Y[k]));
```

$$\pi^{i}{}_{j\,k} = tddiff_{k}(\pi^{i}{}_{j})$$

```
> show(Pi[i,-j,-k]);
```

$$\pi^{i}{}_{j\,k} = 0$$

```
> definetensor(Pi[i,-j,-k,-l]=tddiff(Pi[i,-j,-k],Y[l]));
```



$$\pi^{i}{}_{jkl} = tddiff_l(\pi^{i}{}_{jk})$$

```
> show(Pi[i,-j,-k,-l]);
```

$$\pi^{i}{}_{jkl} = 0$$

```
> definetensor(B[i,-j,-k,-l]=tdiff(Pi[i,-j,-k],X[l])-tdiff(Pi[i,-j
  ,-l],X[k])+Pi[s,-j,-k]*Pi[i,-s,-l]-Pi[s,-j,-l]*Pi[i,-s,-k]+Pi[i,
  -j,-l,-s]*Pi[s,-k]-Pi[i,-j,-k,-s]*Pi[s,-l]);
```

$$B^{i}{}_{jkl} = tdiff_l(\pi^{i}{}_{jk}) - tdiff_k(\pi^{i}{}_{jl}) + \pi^{s}{}_{jk}\pi^{i}{}_{sl} - \pi^{s}{}_{jl}\pi^{i}{}_{sk} + \pi^{i}{}_{jls}\pi^{s}{}_{k} - \pi^{i}{}_{jks}\pi^{s}{}_{l}$$

```
> definetensor(r[-j,-k]=B[i,-j,-k,-i]);
```

$$r_{jk} = B^{i}{}_{jki}$$

```
> definetensor(rho[-j,-k,-l]=tdiff(r[-j,-k],X[l])-Pi[i,-j,-l]*r[-i
  ,-k]-Pi[i,-k,-l]*r[-j,-i]-tdiff(r[-j,-l],X[k])+Pi[m,-j,-k]*r[-m,
  -l]+Pi[m,-l,-k]*r[-j,-m]);
```

$$\rho_{jkl} = tdiff_l(r_{jk}) - \pi^{i}{}_{jl} r_{ik} - \pi^{i}{}_{kl} r_{ji} - tdiff_k(r_{jl}) + \pi^{m}{}_{jk} r_{ml} + \pi^{m}{}_{lk} r_{jm}$$

```
> show(rho[-1,-2,-1]);
```

$$\rho_{x1\ x2\ x1} = 0$$

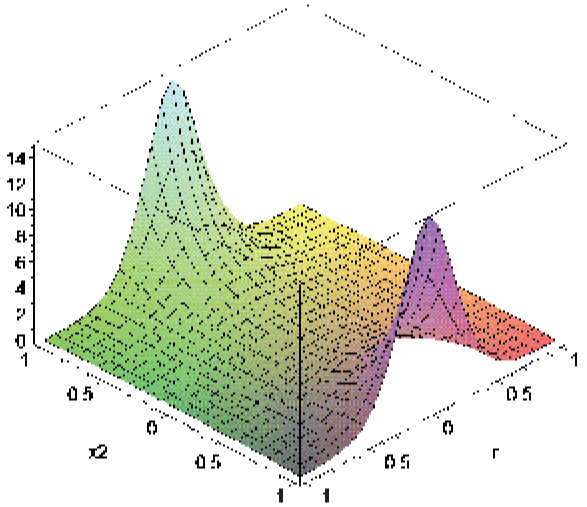
```
> show(rho[-2,-1,-2]);
```

$$\rho_{x2\ x1\ x2} = 0$$

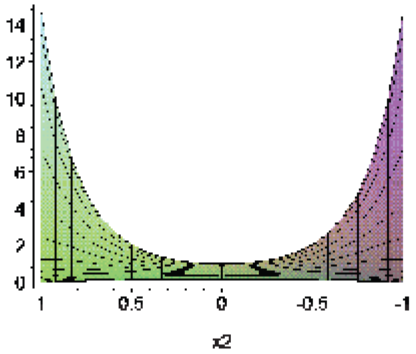
```
> K[par]:=simplify(subs(y1=r*y2,K));
```

$$K_{par} := \frac{e^{(-c\,x2^2)}\,c\,(e^{(-c\,x2^2)} + c\,x2^2\,e^{(-c\,x2^2)} + r^2 - 2\,r^2\,c\,x2^2)}{(r^6 + 3\,r^2\,e^{(-2\,c\,x2^2)} + 3\,e^{(-c\,x2^2)}\,r^4 + e^{(-3\,c\,x2^2)})\,(r^2 + e^{(-c\,x2^2)})}$$

```
> plot3d(subs(c=1,K[par]),r=-1..1,x2=-1..1,axes=boxed,orientation=
  [225,45]);
```



```
> plot3d(subs(c=1,K[par]),r=-1..1,x2=-1..1,axes=boxed,orientation=
  [180,90]);
```



```
> plot3d(subs(c=1,K[par]),r=-1..1,x2=-1..1,axes=boxed,orientation=
  [90,90]);
```

5. The Canalization Idea of Biologist, C. H. Waddington

Following C.H. Waddington, picture the epigenetic landscape,[34], as a curved surface with a deep valley channel down along which a developing embryo roles, bouncing around as it goes, due to developmental noise represented by the e(t)- term in (2). The embryo stays more or less in the valley because development is canalized, but the valleys may branch off and the embryo may go along one or another of these detours subject to noise in the cellular environment. However, there must be some significant external input, perhaps a gradient field or the curl of a vector field, simply because pure randomness would not increase complexity over evolutionary epochs. The epigenetic landscape has a geometry constrained by this external input. For example, situations where cooperation between two independent cell lineages directly affects a 3rd, certainly must arise during ontogeny, but would never happen mathematically, without external influences. At this stage, heterochrony, the time-sequencing change during ontogeny, must play a role. The notion combines allometric concepts with external driving forces, both deterministic and stochastic, giving rise to changes classified as *plastic deformations of the phenotype of a developing embryo*. We now briefly describe the mathematical theory behind these statements,[35],[36].

There has been extensive study of organ growth in animals which indicates that the phenotypic characters of final adult forms are tightly canalized about their means in the statistical sense. Both the distribution of rates of biomass production and total biomass accumulations are of small variance as time of full maturation is approached. The classical experimental work of Nobel physiologist, Sir Peter Medawar, on embryonic chicken heart tissue showed this canalization property, [37]. In fact, Medawar proved that the tissue is well described by a Gompertz growth curve, using sound statistical methods. *A simple model of developmental noise*, which includes the role of measurement error, is:

$$dx(t) = N(t)dt$$

$$dN(t) = -cN(t)dt + \mu^2.dw(t)\ ,$$

where c is the positive growth rate constant and μ is the standard deviation for a zero centered normal distribution. If $\mu = 0$ and x(0) and N(0) are positive initial conditions, this system yields Gompertz solutions, log[m(t)], m being the total Gompertz biomass measured, However, the model with $\mu \neq 0$ yields a divergent variance for x(t) as $t \to \infty$ and a finite variance for N(t), [8, appendix B], [38]. Even if, –ax.dt, a negative linear form, is added to the right-hand-side of the second equation, the divergence problem remains. Therefore, C. H. Waddington's developmental noise is not canalized in this simple, yet reasonable, model.

However, it is possible to rectify this infinities difficulty using the conservative diffusion theory called Nelson Stochastic mechanics, [39]. It is different from regular (i.e., dissipative) diffusion because it confines the Brownian particles to certain regions so it cannot disapate (rather like small material masses in random motion within the rings of Saturn). It will be seen that this theory yields biomass distributions of castes and morphotypes which are stationary in time. The Nelson stochastic mechanics method has been used recently with success in, [48].The first biological application was by M. Nagasawa, [42], but see his monograph,[43].

To begin, take two Gompertzian populations, #1 and #2, like the one above with μ = 0 and further assume each has the same rate constant, c. Using the natural production parameter, s, with ds = (1/c)exp[ct]•dt, straight line allometry is obtained, an equivalent form of Gompertz growth with 2 modes simply expressed as

$$dx^i/ds = y^i\ ,\ \ dy^i/ds = 0, \quad i \in \{1,2\}$$

Now let Q(x) be a (sometimes linear) scalar function of x^1, x^2 and define the *time-change* called a heterochronic transformation (s → p) induced by an external source S^i(x,y).This time-change is specified along any trajectory, γ(s), by the line integral of Q:

$$dp/ds = A.exp\{-\textstyle\int Q\ ds\},$$

where A is an arbitrary constant and

$$d^2x^i/\mathrm{d}p^2 2 + \delta^i{}_j Q_k\ (\mathrm{d}x^j/\mathrm{d}p)(\mathrm{d}x^k/\mathrm{d}p) = S^i.$$

Note that taking Q to be linear, Q = $Q_k x^k$ (summation convention on repeated upper/lower indices) implies that the coefficients of Q are (positive) constants .We use this below, yet much of the discussion leaves Q arbitrary. It is further supposed that over time there will result an energy conservation mode in which S^i reduces to C^i and:

1) (dx/dp)·C = 0 , (Euclidean dot product)
2) $S^i = C^i$ is linear in Q(x).

The first condition ensures vector, C^i will be the curvature vector for the transformed biomass production process. It has to be orthogonal to the trajectory. Also, when it is not zero, it expresses a specific *deformation of the original trajectory*. The second condition allows any function Q(x) to have an additive effect on a transformed one, that is, transformation by Q and by another Q* will be the same as that by, Q + Q*.

These two conditions combine to precisely define the notion of an Adapted Heterochronic Transformation, (AHT). It is a theorem that the energy quantity within DEBT :

$$2\mathrm{E} = \exp\{2Q(x)\}[\,(N^1)^2 + (N^2)^2]$$

is constant along any solution $\gamma(p)$ and solutions are minimizing in the Euler-Lagrange sense,[38],[39].

We compute the curvature/deformation vector components for arbitrary Q to be

$$C^2 = Q_2(N^1)^2 - Q_1(N^1)(N^2)\,,$$

$$C^1 = Q_1(N^2)^2 - Q_2(N^1)N^2)\,,$$

with $N^1 = \mathrm{d}x^1/\mathrm{d}p, \qquad N^2 = \mathrm{d}x^2/\mathrm{d}p,$

$$\mathrm{d}N^1/\mathrm{d}p + Q_1(N^1)^2 + Q_2(N^1)(N^2) = C^1,$$

$$\mathrm{d}N^2/\mathrm{d}p + Q_2(N^2)^2 + Q_1(N^1)(N^2) = C^2.$$

After an initial (AHT) adaptation the system may respond to further external influences, either noisy or deterministic. For example, a gradient field arising from sustained nutritional intake may provide an energy surge contributing to enhanced cellular production. This may be expressed by adding, respectively, to the first and second right-hand-side components, -a.grad^1(Q) and -a.grad^2(Q) for some positive constant denoted, a. Another external effect that can be added is noise. If Nelson's stochastic mechanics is used there will result *distributions stationary in time over the production space*. This is a version of Waddington's canalization. We will now briefly describe this method. The system of Euler-Lagrange equations are

$$-\mathrm{a}Q_1 = \mathrm{d}N^1/\mathrm{d}p + 2Q_2(N^1N^2) + Q_1[(N^1)^2 - (N^2)^2], \quad *$$

$$-\mathrm{a}Q_2 = \mathrm{d}N^2/\mathrm{d}p + 2Q_1(N^1N^2) + Q_2[(N^2)^2 - (N^1)^2], \quad **$$

with a linear Q function. If we set, a = 0, these equations, adjoined with $N^i = \mathrm{d}x^i/\mathrm{d}p$, become geodesics of the Riemannian geometry(J=0) whose arc-length functional is just the square root of the energy expression 2E, above, namely,

$$dp = \exp\{Q(x)\}.\surd[(dx^1)^2 + (dx^2)^2].$$

Furthermore, we can define a potential V(x) by:

$$V(x) = (a/2)\exp\{2Q(x)\},$$

whose gradient is:

$$g^{ir}\partial_r V(x) = aQ^i,$$

where,

$$g_{ij}(x) = \exp\{2Q(x)\}\delta_{ij},$$

is the inverse matrix, i. e.,

$$g^{ik}.g_{km} = \delta^i_m$$

Note that the energy expression, 2E, above can be written as the sum of quadratic differential forms (an averaging over the 2 independent modes of change, dx^1 and dx^2,

$$(dp)^2 = g_{nm}dx^n dx^m,$$

and that the curvature/stability measure, K, is actually the Riemann scalar curvature, R, of classical Riemannian geometry. It is completely specified by the matrix, g, and its partial derivatives with respect to x^i, up to 2nd order, [40],[41].

Using the calculus of variations to obtain the Euler–Lagrange equations for fixed (starting time and finishing time)-variation of the integral:

$$\int[\,[(½)\exp\{2Q(x)\}\cdot\{\,(dx^1/dt)^2 + (dx^2/dt)^2\} - V(x)\,]\,dt\,,$$

the system above with the gradient on the right-hand-side is obtained.

In order to bring noise into this formalism one considers the Nelson Expectation,[42],[43], of the above expression, namely,

$$EN\{\int[(1/2).\,g_{ij\,(a(t))}\,\mathring{a}i_{(t)}\,\mathring{a}j_{(t)} - V(a(t))].dt\}$$

defined by the infinitesimal generator, which is an operator of the form

$$(1/2)\mu.\Delta_g + \mathrm{grad}\cdot b(x,t),$$

using the g- Laplacian (relative to Riemannian geometry for, dp, above) and where a(t) and its dot derivative form an inhomogeneous Markov diffusion (the circle dot indicates the velocity) with initial time density ρ(x,t') and initial time drift vector b(x,t'). The Nelson stochastic variation of B(a), (with drift variation vanishing at initial and final times) gives the Newton-Nelson Equation:

$$½(\,DD^* + D^*D)(a(t)) = -\mathrm{grad}\,V(a(t)),$$

with:

$$DY = \mathrm{Lim}\,(1/h)EN\{\,Y(t+h) - Y(t)\,|\,P_t\},$$

as h→ 0 from the right and, likewise,

$$D^*Y = \mathrm{Lim}\,(1/h)EN\{\,Y(t) - Y(t-h)\,|\,F_t\},$$

as h→ 0 from the right.

Here, F_t and P_t are the future and past sigma algebras

$$F_t = \sigma\{a(s)\,|\,t \le s\},$$

$$P_t = \sigma\{a(s)\,|\,t \ge s\}.$$

The fundamental result in Nelson mechanics is that the Newton-Nelson equation is equivalent to the partial differential equation:

$$i(\sqrt{\mu})\partial\Theta(x,t)/\partial t = [- (½)\mu\Delta_g + V(x) - (\mu/12)K]\Theta(x,t),$$

where i is the unit length imaginary number. Furthermore, this equation is of Schrӧdinger type with:

$$b(x,t) = \sqrt{\mu}.(Im + RE)[(1/\Theta(x,t)).grad\Theta(x,t)],$$

and:

$$\rho(x,t) = |\,\theta(x,t)\,|^2,$$

the square of the complex modulus of Θ. The quantity, $(1/2)\nabla\ln\rho, is\ called\ the\ osmotic\ velocity.$

The so-called Stationary Solutions, are of the form:

$$\Theta(x,t) = \exp\{-i\gimel t\}(f_{\gimel})(x),$$

and they solve the eigenvalue problems for eigenvalues ,$\gimel$,

$$— (1/2)\mu.\Delta_g(f_{\gimel}(x)) + V(x)f_{\gimel}(x) – (\mu/12).K.f_{\gimel}(x) = \gimel f_{\gimel}(x).$$

In the linear case of Q(x) it is readily found that, K = 0. Because there is a coordinate transformation from (x^1,x^2) to polar coordinates (r, θ) and the starred equations above can be written:

$$d^2\theta/(ds)^2 - r(d\theta/ds)^2 = -kr$$

$$d^2\theta/ds^2 + (2/r)(dr/ds)(d\theta/ds) = 0$$

where $k = a(Q_1^2 + Q_2^2)$ and $s(t) = A – B.\exp\{-\gimel t\}$ and $r = \exp\{Q\}$, $\theta = (Q_1, Q_2)\cdot(-x^2, x^1)$, the latter being a Euclidean dot product.

It now follows that the eigenvalue problem can be written:

$$(1/2)\mu\,\Delta_{polar}f_{\gimel}(r) + (k/2)r^2 f_{\gimel}(r) = \gimel f_{\gimel}(r).$$

This is a discrete eigenvalue problem whose lowest eigenvalue is $\gimel_0 = \sqrt{(\mu a)}$ with corresponding eigendensity:

$$f_0 = C_0\exp\{-(1/2)\sqrt{[a/\mu]}r^2,$$

which is well known. The rest of the eigenvalues are given by $\gimel_n = \sqrt{[a\mu]}(n + 1)$ while the corresponding eigenfunctions become very complicated and represent distributions of allometric variables of higher and higher energy,[42],[43],[44].The distributions can be compared to mountain ranges. As $\gimel$ increases through discrete values the mountain peaks increase in number exhibiting greater variability in phenotypic expression. The publications,[15],[42],[43], [48] contain more information on stochastic mechanics.

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