DIFFERENTIAL GEOMETRIC METHODS IN ECOLOGY *

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Resumo

Neste artigo apresentamos uma revisão da abordagem analítica da Trofodinâmica, consistindo tanto de equações ecológicas quanto de equações de produção de Volterra. Uma breve descrição dos conceitos geométricos utilizados, bem como da história de modêlos ecológicos e afins, é também apresentada. Como exemplo, abordamos um moêlo da floresta climática de Clements e do processo de sucessão, baseado um paralelo traçado com o processo de desenvolvimento embriológico e do mecanismo de heterocronia. Todos cálculos foram realizados pelo pacote de computação algébrica FINSLER, escrito sobre o Maple.

Abstract

In this paper we present a review of the analytical approach to Trophodynamics, consisting of both ecological equations and Volterra production equations. Some background material on differential geometry, as well as an historical sketch are also presented. As an example, we propose a model of Clements' climax forest and the process of succession based on a parallel with embryological development and the mechanism of heterochrony. All calcutations were performed by the computer algebra software FINSLER, based on Maple.

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1 Introduction.

Given a smooth connected n-dimensional manifold M^n with local coordinates $(x^1, \ldots, x^n)$, the collection of tangent vectors (to curves $x^i = x^i(t)$, $i = 1, \ldots, n$ in M^n) at some point $P(x^i) \in M^n$ defines the *tangent space* $T_P M$ at P. The collection of all tangent vectors to M^n defines TM, the *tangent bundle* of M. Letting (x^i, N^i) denote the natural phase space coordinates on TM, consider the 2nd order system of ordinary differential equations (SODE)

$$\begin{cases} \dfrac{dx^i}{dt} = k_{(i)}\ N^i \qquad \text{(not summed)} \\[2ex] \dfrac{dN^i}{dt} = -\Gamma^i_{jk}\ N^j N^k + r^i_j\ N^j + e^i, \end{cases} \tag{1.1}$$

where repeated indexes are summed (unless otherwise stated), all coefficients (possibly) depend on (x^i, N^i, t), the n^3 functions Γ^i_{jk} are homogeneous of degree zero in N^i, and with smooth initial conditions (x^i_0, N^i_0, t_0). For almost 20 years this system has played a major role in mathematical theories of ecology, evolution and development in colonial invertebrates, and also in epidemiology [9], [2], [5]. The coordinates x^i are Volterra's production variables, whose constant per capita rate of increase is k_i, while the 2nd part of the system is a description of how different species or sub-populations of a colonial organism (i.e. castes) $N^i \geq 0$ *grow* (r^i_j), *interact* (Γ^i_{jk}) and *react* (e^i) to external influences. In the ecological context, this scheme must entail competition, symbiosis or parasitism, while predator effects usually require additional equations coupled to (1.1). The condition that Γ^i_{jk} are functions of *ratios* of N^i, stated above, indicates the presence of so-called *social interactions*, which are higher-order, *density dependent effects*. Whereas classical ecological theory would have Γ^i_{jk} merely constants, the theory of density dependent social interactions, initiated by G. E. Hutchinson in 1946 [26], [25], found experimental verification in the subsequent work of Wilbur, Hairston and others [39], [40], [23]. In 1991, work developed by Antonelli and Bradbury [7], [8] indicated that Hutchinson's theory should be recast using zero degree homogeneous interactions (Γ^i_{jk}) in order to be consistent with experimental data. Unfortunatelly, the mathematical approach that Hutchinson had used originally was intractable and his theory lay fallow for more than 40 years. Thus, 1991 marks the birth of a mathematically accessible theory of Hutchinsonian social interactions, and also the realization that *Finsler geometry describes cost-effective growth and physiology in socially interacting colonial organisms* like siphonophores, ants and other social insects, as well as many marine species (Acropora corals). It also has been applied to the myxomatosis disease epidemic model [13], [3], [11]. Furthermore, the addition of noise to Volterra-Hamilton theory, as described by (1.1), has been successfully acomplished, a complete description being found in [3]. An introductory text on the subject as a whole can be found in the textbook by Antonelli and Bradbury [11].

Recently this approach to ecology and related subjects, as well as geometrical modelling in general, particularly making use of Finslerian geometries and/or systems of 2nd order ordinary differential equations (SODE), have been substantially facilitated by means of a purpose-developed computer algebra package named FINSLER [34], based on Maple [30]. This software, in its present version, derives the expressions of geometrical objects from a given (metric) function or connection (i.e. SODE), which, in the context of this paper, are ecologically interpreted in terms of stability of the system under consideration. Some new results on well known ecological models have recently been obtained by means of this package and other softwares available within Maple, in a work currently in progress [15].

2 Ecological models: an historical perspective.

Let us begin by describing the first attempts at modelling simple growth of (isolated) populations, or those whose behaviour can be seen as independent of their interactions with other species and/or environmental effects. Those were based on three simplifying assumptions, namely, that the rate of increase (decrease) of the population size (or density) is a differentiable function of the population size (density) itself,

$$\frac{dN}{dt} = f(N), \quad f \text{ differentiable.} \quad (I)$$

Secondly, it is assumed that there is no spontaneous generation, or if

$$N = 0 \quad \text{then} \quad \frac{dN}{dt} = 0. \qquad (II)$$

Finally, one should consider that there is a limit to the population size, given that space and/or resources are themselves finite,

$$N \leq N_{max} \text{ for any given } t. \quad (III)$$

Given such assumptions, we can readily expand $f(N)$ in powers of N, obtaining

$$\frac{dN}{dt} = a + b\ N + c\ N^2 + \ldots,$$

where a, b, c are constants, and assumption (II) implies $a = 0$.

The 1st and simplest population model was proposed by Malthus and considered this series only up to the linear term, giving an exponential growth as result

$$\frac{dN}{dt} = b\ N \ \Rightarrow\ N = N(0)\ e^{bt}, \quad b > 0.$$

Although this model does not conform to the 3rd assumption above, it gives a good representation of unbounded growth, particularly at early times, when a population has all resources needed and no restrictions to its expansion.

Proceeding to consider the power expansion up to 2nd order, renaming $b = \lambda$ and $c = -\lambda/K$ (λ and $K > 0$ being the so-called *intrinsic growth rate* and *carrying capacity* for N, respectively) we get the the well-known *logistic equation*, which yields the *logistic curve.*

$$\frac{dN}{dt} = \lambda N \left(1 - \frac{N}{K}\right) \ \Rightarrow\ N(t) = \frac{K}{1 + be^{-\lambda t}}$$

This S-shaped curve does conform to all 3 assumptions above, and models finite resources growth, and is of frequent use in many fields, from biology to economics. Increasing exponentially at early times, N changes inflection at $K/2$, and tends to the limit $N_{max} = K$ as t increases.

We shall be using as well the notion of *allometric growth*, as proposed by Huxley in 1932, by which a species growth preserves a proportionality among its parts. Considering growth unlimited by resources, and say $x(t) = Ce^{\alpha t}$ is a measure of the diameter of a tree. Then, if $y(t) = De^{\beta t}$ is the total leaf biomass in the same tree, then we have that $x^{\beta/\alpha} = C^{\beta/\alpha}e^{\beta t}$, or

$$y = M\ x^{\beta/\alpha}, \quad M = \frac{D}{C^{\beta/\alpha}},$$

and β/α is *characteristic of each species* at a particular location. In practice, $x(t)$, $y(t)$ are avarage values from a sample, thus y may be estimated from x from just a small randomly selected sample. This is a standard technique in forestry for estimating crown biomass of a stand.

If there is need to consider resource limited growth, then we will have $x = K/(1 + be^{-\alpha t})$, $y = L/(1 + ae^{-\beta t})$, leading to

$$y = \frac{L}{a\left(\frac{K-x}{bx}\right)^{\beta/\alpha} + 1}.$$

We can see that the system approaches equilibrium when $x, y \to K, L$ respectively, so, defining new *relative proportion* variables $x^* = (K - x)/x$, $y^* = (L - y)/y$, we get Malthusian-like equations for these, and therefore exponential decrease $x^* = be^{-\alpha t}$, $y^* = ae^{-\beta t}$, thus leading to a *relative proportion Huxley allometric law* which looks the same as before

$$y^* = M^*\ (x^*)^{\beta/\alpha}, \quad M^* = \frac{a}{b^{\beta/\alpha}}.$$

We shall be using these alternative variables in an important example in section 4.

Now, consider that a species population's growth may be affected by some other's. These so-called *ecological interactions* have been classically considered to fall into 3 possible categories, namely, as their interaction goes on:

- *predator-prey:* growth rate of one species goes up, the other down;
- *competition:* both rates down;
- *symbiosis:* both rates up.

The 1st and simplest model of such interactions was proposed by Volterra in 1926 to explain the cycling behaviour observed in fish populations in the Adriatic sea. Let N be the prey population size and P the predator's. Then their dynamic would be given by

$$\begin{cases} \dfrac{dN}{dt} = N\ (a - bP) \\ \\ \dfrac{dP}{dt} = P\ (cN - d), \end{cases} \tag{2.2}$$

where all parameters are positive constants. This model express the following basic assumptions:

(i) prey population without predation grows unboundedly (aN term);

(ii) predators reduce prey population proportionally to both populations ($-bNP$ term);

(iii) without predation, predator population decreases exponentially ($-dP$ term);

(iv) prey's effect in predator population proportional to both populations ($+cNP$ term).

This model predicts an unstable oscillatory behaviour for both populations, prey's peaking ahead of the predator's. A modern and more sophisticated version of the same interaction was proposed [9], [2] for starfish predating on coral on the Great Barrier Reef,

$$\left\{\begin{aligned} \frac{dN}{dt} &= \lambda N - \alpha N^2 - \delta NF \\ \frac{dF}{dt} &= -\epsilon F + \gamma F^{p+1} + 2\beta NF, \end{aligned}\right. \tag{2.3}$$

predicting stable limit cycle for $1/2 < p < 1$, which is non-existent if $p > 1$. The new mechanisms considered here are the *aggregation* (γ) and *reproductive potential* (p) of the starfish (predator) population F. The 2nd order term (not mixed) in each equation comes from logistic growth, and is corrected by these mechanisms in the predator's population. Parameters are again constants.

We call a *trophic web* Σ the community of n interacting species. Considered 2 by 2 at a time, if they don't interact, we have

$$\frac{dN^i}{dt} = \lambda_{(i)}\; N^i \left(1 - \frac{N^i}{K_{(i)}}\right); \quad i = 1, \dots, n.$$

If they compete,

$$\left\{\begin{aligned} \frac{dN^1}{dt} &= \lambda_{(1)} N^1 \left(1 - \frac{N^1}{K_{(1)}} - \delta_{(1)} \frac{N^2}{K_{(1)}}\right) \\ \frac{dN^2}{dt} &= \lambda_{(2)} N^2 \left(1 - \frac{N^2}{K_{(2)}} - \delta_{(2)} \frac{N^1}{K_{(2)}}\right), \end{aligned}\right. \tag{2.4}$$

where the last terms are interaction (non-logistic) terms. If these were both positive, we would have a symbiotic system, and if one were positive and the other negative, a parasitic system. The system (2.4) models the famous competitive exclusion principle whereby only one of the 2 species survives [8].

3 Geometrical Background.

Consider a smooth connected n-manifold M^n and select a chart (U, h) on M^n for the slit tangent bundle $\tilde{T}M^n$ (i.e., without the zero section).

A *local spray* in (U, h) is a system of ordinary differential equations (SODE)

$$\frac{d^2x^i}{ds^2} + 2G^i\left(x, \frac{dx}{ds}\right) = 0 \quad (i = 1, \dots, n), \tag{3.5}$$

where the n functions G^i are C^∞ on U in x^i and dx^i/ds (off the zero section), otherwise continuous and 2nd degree positively homogeneous in dx^i/ds.

For an arbitrary parameter t along solutions of (3.5) we have the SODE

$$\ddot{x}^i + 2G^i(x, \dot{x}) = \frac{s''}{s'}\, \dot{x}^i, \tag{3.6}$$

where $s' = ds/dt$, $s'' = d^2s/dt^2$, $\dot{x}^i = dx^i/dt$, $\ddot{x}^i = d^2x^i/dt^2$. Consider the canonical spray connection coefficients in (U, h):

$$G^i_j = \dot{\partial}_j G^i, \quad G^i_{jk} = \dot{\partial}_k G^i_j, \tag{3.7}$$

where $\dot{\partial}_l$ indicates differentiation with respect to $\dot{x}^l$. A transformation of variables from (U, h) to $(\bar{U}, \bar{h})$, i.e. $(x^1, \ldots, x^n) \to (\bar{x}^1, \ldots, \bar{x}^n)$ has the effect

$$\frac{\partial \bar{x}^r}{\partial x^j}\frac{\partial \bar{x}^s}{\partial x^k}\, \bar{G}^i_{rs} = \frac{\partial \bar{x}^i}{\partial x^r}\, G^r_{jk} \; - \; \frac{\partial^2 \bar{x}^i}{\partial x^j \partial x^k} \tag{3.8}$$

in the overlap region between U and $\bar{U}$. Because G^i are homogeneous of 2nd degree in $\dot{x}^l$, we may have, equivalently to (3.5),

$$\frac{d^2x^i}{ds^2} + G^i_{jk}\left(x, \frac{dx}{ds}\right)\, \frac{dx^j}{ds}\, \frac{dx^k}{ds} = 0. \tag{3.9}$$

We may also define $I\!\!D^i_{jkl} \equiv \dot{\partial}_l G^i_{jk}$, the Douglas tensor, which transforms as a 4th-rank tensor. The importance of $I\!\!D$ lies in the fact that G^i_{jk} are independent of $\dot{x}^l$ if and only if $I\!\!D^i_{jkl} = 0$, i.e., the vanishing of $I\!\!D$ is necessary and sufficient for G to be a quadratic spray, as in classical affine geometry and its specialization to Riemannian geometry. Its vanishing is equivalent to the existence of normal coordinates $\tilde{x}^i$ at each $P \in M^n$, in terms of which the transformed connection coefficients $\tilde{G}^i_{jk}$ are zero at P, and therefore we have straight lines through P. If the normal coordinates $\tilde{x}^i$ represents $\log(m^i)$ then we recover Huxley's allometric law. In this case (3.9) is to be regarded as nonlinear allometric growth.

Under transformation of variables, we define the *KCC-covariant derivative* (after Kosambi, Cartan and Chern [29, 21, 19]) of a vector field ξ^i defined along a curve $\gamma(s)$ in M^n as

$$\frac{D\xi^i}{ds} = \frac{d\xi^i}{ds} + G^i_r \xi^r. \tag{3.10}$$

Having defined a covariant derivative of a vector field allows us to introduce the notion of *parallel transport*. We say a vector field $\xi^i(s)$ defined along a curve $\gamma : x^i = x^i(s)$ is parallel transported along γ if $D\xi^i/ds = 0$, using $G^i_r(x(s), \dot{x}(s))$ in (3.10). If the intrinsic parameter s, for which equation (3.5) above holds, is associated with a definition of distance in the manifold, i.e., a metric function is imposed on M^n,

$$ds = F(x, \dot{x}), \tag{3.11}$$

where F is itself homogeneous of degree 1 in $\dot{x}^i$, then, similar to straight lines in plane (Euclidean) geometry, geodesics of F will be *autoparallel curves*, $D^2x^i/ds^2 = 0$, i.e., their tangent vectors dx^i/ds are parallel transported along the geodesics. Solutions of (3.9) (or (3.5)) will be *geodesics* of M^n if we replace G^i_{jk} by

$$\Gamma^i_{jk} = g^{ih}\left[\frac{1}{2}\left(\frac{Dg_{hj}}{\partial x^k} + \frac{Dg_{hk}}{\partial x^j} - \frac{Dg_{jk}}{\partial x^h}\right)\right],$$

where g^{ih} is the inverse of g_{ih}, $g^{ih} = (g_{ih})^{-1}$, and

$$\frac{D}{\partial x^i} = \frac{\partial}{\partial x^i} - G^j_i \frac{\partial}{\partial \dot{x}^j}.$$

If a metric (3.11) is defined on M^n we say that it is a *Finsler space*, or that we have a *Finsler geometry* on M^n. Due to Euler's theorem on homogeneous functions, we can write

$$F^2(x, \dot{x}) = \left(\frac{1}{2} \frac{\partial F^2}{\partial \dot{x}^i \ \partial \dot{x}^j} \right) \ \dot{x}^i \dot{x}^j \equiv g_{ij}(x, \dot{x}) \ \dot{x}^i \dot{x}^j, \tag{3.12}$$

or $ds^2 = g_{ij}(x, dx) \ dx^i dx^j$. The homogeneity condition is necessary and sufficient for the total distance along a curve $x^i = x^i(t)$,

$$s = \int_{t1}^{t2} F \left(x, \frac{dx}{dt} \right) \ dt$$

to be independent of the chosen parametrization. This condition induces dependence on *proportions* or *rates* $(\dot{x}^i / \dot{x}^j)$. This fact will be very convenient to model *social interactions*, as we shall see in the following section.

Another important result that makes Finsler geometry particularly well suited for ecological modelling is that, for each of the 3 possible classical interactions (2.4), there is a "constant of the motion" [14] which constitutes a Finsler metric function and plays the role of *cost per unit of production s*. This result is known as the *Division of Labour theorem*, and solutions of the SODE (2.4) are not geodesics of this cost function, meaning that the process is not perfectly optimal. For more details as how to relate Finsler variables x^i to biomass (or energy, etc) production/consumption for each polulation N^i, see the next section.

Using (3.10), we can reexpress (3.5) [or (3.9)] as

$$\frac{D\dot{x}^i}{dt} = -\epsilon^i = G^i_r \ \dot{x}^r - 2G^i. \tag{3.13}$$

The contravariant vector field ϵ^i is the *1st KCC invariant* of the SODE under transformation of coordinates. $\epsilon^i = 0$ is a necessary and sufficient condition for G^i to be positively homogeneous of degree 2 in $\dot{x}^i$, i.e., the SODE to be a spray. Of course, we will have this if and only if $t = as + b$, with constant a, b.

Varying solutions of (3.5) into nearby ones,

$$\bar{x}^i(t) = x^i(t) + \xi^i(t) \ \eta, \tag{3.14}$$

where $|\eta|$ is small and $\xi^i(t)$ a contravariant vector field defined along $\gamma(t)$. Letting $\eta \to 0$ yields the variational equations

$$\frac{d^2\xi^i}{dt^2} + 2G^i_r \ \frac{d\xi^r}{dt} + 2 \left(\partial_r G^i \right) \ \xi^r = 0, \tag{3.15}$$

which, in invariant form, are

$$\frac{D^2\xi^i}{dt^2} + I\!\!B^i_r \ \xi^r = 0, \tag{3.16}$$

where

$$I\!\!B^i_j = 2\partial_j G^i + 2G^r G^i_{jr} - \dot{x}^r \partial_r G^i_j - G^i_r G^r_j. \tag{3.17}$$

This tensor is the *2nd KCC invariant* of the system (3.5). We can understand $\mathbb{B}^i_j$ as an invariant measure of the *deviation* between the 2 curves concerned, i.e., how much one departs from the other. If those curves represent the evolution in time of the production level $x^i(t)$ of 2 interacting species, then $\mathbb{B}^i_j$ will naturally measure the *stability* of such system in the Jacobi sense, that is, if they have close initial conditions $x^i(t_0) = \bar{x}^i(t_0),\ \dot{x}(t_0) \approx \dot{\bar{x}}(t_0)$ (that is, the populations sizes $N^i(t_0) \approx \bar{N}^i(t_0)$) at some point $P(t_0)$, then they will remain close with increasing t, $x^i(t) \approx \bar{x}^i(t)$. This happens if we have positive eigenvalues for $\mathbb{B}^i_j$. The 3rd, 4th and 5th invariants are, respectively,

$$\begin{cases} \mathbb{B}^i_{jk} = \frac{1}{3}\left(\dot{\partial}_k \mathbb{B}^i_j - \dot{\partial}_j \mathbb{B}^i_k\right) \\ \\ \mathbb{B}^i_{ljk} = \dot{\partial}_l \mathbb{B}^i_{jk} \\ \\ \mathbb{D}^i_{jkl} = \dot{\partial}_l G^i_{jk}, \end{cases} \tag{3.18}$$

where $\mathbb{D}$ is the already mentionated Douglas tensor. Two systems (3.5) are equivalent under transformation of variables if and only if the 5 KCC invariants are equivalent. There exists coordinates in M^n for which G^i all vanish if and only if all KCC invariants are zero. The 4th invariant generalizes the 4-index curvature tensor of Riemannian and Affine geometry.

4 Analytical Trophodynamics.

In 1977, J. L. Harper [24] had already pointed out that, because of their great plasticity, to describe the dynamics of plant communities one would need total biomass (e.g., primary production) as well as population numbers. So, we shall move now from the classical ecological field, which deals with populations sizes only, to one that takes into account the populations' production (consumption) in the description of their interactions. This other field is called *trophodynamics*, dealing with the population dynamics of ecologically interacting species and their production (consumption). This field divides naturally in 2 different approaches: *empirical trophodynamics*, which proposes 'stock and flows' models (stock of biomass, consumption/production of caloric energy, etc) to study their transformations in the ecosystem, and *analytical trophodynamics*, which links ecological equations (competition, etc) to (Volterra) production equations, seeking an analytical approach to ecological modelling. The first approach to trophodynamics is concerned with refining field measurements and with determining the transformation between surrogates variables of biomass. The latter seeks to determine the underlying properties of the dynamics, such as production stability, species interaction patterns and their efficiency, etc, their intrinsic characteristics being described by *curvatures*, geometrical objects assossiated with the *complete specification of the Jacobi stability* of production/consumption processes.

As an example, consider the Harper, Clatworthy and Leslie experiment with simple aquatic plants [24], where the total biomass was fitted with the Gompertz growth curve. This empirical curve is the unique solution (assuming positive initial conditions) to

$$\frac{d^2x^*}{dt^2} + \lambda\ \frac{dx^*}{dt} = 0, \quad \Rightarrow x^* = \ln\, m = \ln\, a - c\ \mathrm{e}^{-\lambda\ t}.$$

Let us now consider the population of fronds to be given by *relative proportion* variables, as in the end of section 2, instead of being population size or density N. Then $N^* = (K-N)/N$ induces a local splitting of the above Gompertz SODE, namely,

$$\begin{cases} \dfrac{dx^*}{dt} = N^* \\ \\ \dfrac{dN^*}{dt} = -\lambda\ N^*. \end{cases} \tag{4.19}$$

The 2nd equation is equivalent to the logistic for N, $dN/dt = \lambda\ N(1-N/K)$, which agrees with Harper's conception of a plant as a population of modular units, in this case, fronds.

In order to make a mathematical model for trophodynamics, we shall introduce Volterra's production (consumption) variable $x^i(t)$ [1][1], a quantity produced by each species that may affect the ecological and/or environmental G^i_{jk} interactions in the trophic web Σ,

$$x^i(t) = l_{(i)} \int_0^t N^i(t)dt + x^i(0), \tag{4.20}$$

where N^i is the size of the ith population, l_i a positive constant and x^i are surrogates variables of biomass, which measure the production of biomass (secondary componds for defence, etc.) or consumption of energy (measured as caloric energy, forms of carbon, wet weight, etc.).

Classical ecological equations and Volterra production equation combine to yield a *2nd order system of ordinary differential equations* (SODE) known as Volterra-Hamilton systems [11], [6]:

$$\begin{cases} \dfrac{dx^i}{dt} = k_{(i)}\ N^i \\ \\ \dfrac{dN^i}{dt} = \lambda_{(i)}\ N^i - G^i_{jk}\ N^j N^k, \end{cases} \tag{4.21}$$

(where, in this case, the G^i_{jk} are n^3 positive constants) yielding

$$\frac{d^2x^i}{dt^2} + G^i_{jk}\ \frac{dx^j}{dt}\frac{dx^k}{dt} = \lambda\frac{dx^i}{dt}. \tag{4.22}$$

If we now take $ds = e^{\lambda t}dt$ (such that $(d^2s/dt^2)/(ds/dt) = \lambda$), where s is called the *intrinsic production parameter*, we get

$$\frac{d^2x^i}{ds^2} + G^i_{jk}\ \frac{dx^j}{ds}\frac{dx^k}{ds} = 0, \tag{4.23}$$

which is known as a *constant spray*, as in the previous section. For $n = 2$ we reproduce the ecological equations once we go from production parameter s back to the usual (time) parameter t. Volterra-Hamilton

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[1] Note that both x^* and $x^i(t)$ here defined are surrogate measures of biomass, but, although related, these are not the same. See [13]

systems, therefore, are the generalized mathematical framework proper to deal with trophodynamical theories. In fact, this framework admits further generalizations, such as $G^i = G^i(x,\ N,\ t)$, which hold biological meaning, thus leading to more sofisticated and (hopefully) precise models.

The aquatic plants considered in (4.19) exhibit chemical defenses under laboratory conditions [4]. For an explicit model of chemical influences based on a Volterra-Hamilton system, we shall consider, following [11], page 62, a plant's chemical defense against herbivory according to Rhoades' Theory of Optimal Defense. Such a model would be

$$\frac{d^2x}{dt^2} + \left(\frac{\lambda}{K} + gx\right)\left(\frac{dx}{dt}\right)^2 - \lambda\frac{dx}{dt} = 0 \tag{4.24}$$

or, in Volterra-Hamilton form, using Volterra variable x,

$$\begin{cases} \dfrac{dx}{dt} = N \\ \\ \dfrac{dN}{dt} = \lambda\ N - \left(\frac{\lambda}{K} + gx\right) N^2, \end{cases} \tag{4.25}$$

where $g > 0$ is Rhoades' parameter which indicates strong plant response when $g << 1$. Switching to the spray parameter we have

$$\frac{d^2x}{ds^2} + \left(\frac{\lambda}{K} + gx\right)\left(\frac{dx}{ds}\right)^2 = 0. \tag{4.26}$$

The 5 KCC-invariants are now easily computable. Using FINSLER, we get that they all vanish, meaning that the chemical production is unstable in Jacobi sense, i.e., weakly chaotic. This is in accord with Rhoades' Theory of Optimal Defense. For multiple species chemical interaction models, please see [11].

We shall now introduce the notion of *social interactions*, which considers higher order terms than the usual 2nd order ones of classical ecological interactions. Literature in the subject begins in 1946, when Hutchinson [26], [25] proposed that cubic terms should replace classical quadratic terms in the 2-species competition equations. Statistical evidence from field data to support the need for higher order terms was produced later [39], [40], [23]. Wilbur states explicitly not only that "higher-order interactions were as important as main (ecological) effects", but there was evidence of "a complex interaction between *proportions* as well as the abundances and the identity of the species". Therefore, following [7], [8], we shall model social interaction terms as (positively) *homogeneous of 2nd degree* in N^i, so that they *scale as quadratic* terms. These will frequently involve proportions (N^i/N^j), such as

$$\left(\frac{N^2}{N^1}\right)^4 (N^2)^2 \Rightarrow \left(\frac{\lambda N^2}{\lambda N^1}\right)^4 (\lambda N^2)^2 = \lambda^2 \ \left[\left(\frac{N^2}{N^1}\right)^4 (N^2)^2\right], \quad \lambda > 0,$$

conforming to Wilbur's findings above.

As a example of application of a Volterra-Hamilton system with social interactions, we will choose a model of interaction between two species of corals in the Great Barrier Reef of Australia [7], [12].

$$\begin{cases} \dfrac{d^2x^1}{ds^2} - \left[-\alpha_1(N^1)^2 - \alpha_2\ \dfrac{m}{m-1}\ N^1N^2 - \alpha_1\ \dfrac{(N^2/N^1)^{(m-2)}}{m-1}\ (N^2)^2\right] = 0 \\ \\ \dfrac{d^2x^2}{ds^2} - \left[-\alpha_2(N^2)^2 - \alpha_1\ \dfrac{m}{m-1}\ N^1N^2 - \alpha_2\ \dfrac{(N^1/N^2)^{(m-2)}}{m-1}\ (N^1)^2\right] = 0. \end{cases} \tag{4.27}$$

This system is stable. For reference, please see *ibid.*

5 Modelling Succession.

In 1915 the American ecologist F. E. Clements, conceived of a forest as a superorganism with a characteristic development analogous to the embryological development of an individual. Each has a time-sequence of events: *succession* being a series of ecological stages, which we here and from now on in this paper call *ecoscenes*, that a forest goes through until it reaches a *climax*, whereas a series of ontogenetic stages culminates in an adult phenotypic individual. This climax forest would be optimal for the ambient climate.

Previous work of ours on both succession in a forest and ontological development in an individual [11, 18] has suggested: whereas development in an individual may be viewed as a series of genetically controlled events allowing response to environmental influences, no such genetic control is available to a forest as a whole. Moreover the concept of time-sequencing changes in the development of an individual, called *heterochrony*, is an important evolutionary process and evidence for it is found in the fossil record [31, 32]. But, for a forest, the notion of a phyletic line of fossils must be replaced by the concept of a *sere*, which is a progressive series of ecoscenes. For a sere the ecological / physiological interactions between populations of plants in an ecoscene are transformed into a new interaction pattern in a new *ecoscene*. The ecoscene in Clements' view is a product of the climate and is controlled by it. The new interactions may be very different, but eventually the climax formation is reached. This is analogous to the adult stage in development of an individual. No further major changes in community structure occurs in Clements' *monoclimax* theory. For historical account, see [37], [20] and [36].

6 Clements' Concept of Succession.

As vegetation develops in an area, that area becomes successively occupied by different plant communities, each an ecoscene, in our terminology. Within a region, the final stage or climax results from the series of successive stages, and regardless of whether it starts in open water, solid rock or denuded land, the resulting climax is the same. Successions beginning in ponds, lakes, marshes or elsewhere in water constitute a hydrosere. The movement from one stage of the sere to the next is usually continuous, but when one dominant group of plants gives way to another, the change is clear. For example, floating plants give way to reeds and rushes. In fact, a hydrosere begins with submerged plants, which are gradually replaced by floating plants, this followed by a sedge meadow, then woodland and finally the climax forest.

The plant *formation* is the major unit of vegetation. It does not include animals, for this the word *biome* is used. The formation can be continental in scope, and is a fully developed climax community of a natural area. The formation is a complex and definite organic entity with a characteristic development and structure. It is a product of the climate and is controlled by it. The deciduous forest of the eastern

USA, the coniferous forest of the Great Lakes region, the tundra of the far north of Alaska and Canada, and the grasslands of Saskatchewan and Manitoba are all examples. A formation arises, grows, matures and finally dies. It is able to reproduce itself, as may be seen after fire, lumbering or other catastrophes to vegetation.

The visible unity of a climax forest is due primarily to the *dominants* or controlling species of plants. In prairie and steppe, it is the grass form, i.e., the climax dominants are all grasses and sedges. The shrub life form characterizes the 3 scrub climaxes of North America, namely, the desert, sagebrush and chaparral forms. The tree life form appears as coniferous, deciduous and broad-leaved evergreen, each of which corresponds to the boreal, the temperate and the tropical climax forests, respectively.

Just as each stage in succession (i.e., ecoscene) has its temporary or seral dominants, so each formation has its climax dominants. Each formation is named after 2 of its most widely spread and important dominants. Examples are cedar-hemlock (coast forest climax) and spruce-larch (boreal forest climax). Every climax formation consists of 2 or more major subdivisions Clements called *associations.* These are climax communities associated regionally to constitute the formation. *The number of associations is determined by the number of subclimates within the general climate of the formation.* Furthermore, each association is marked by one or more dominants peculiar to it. Often, there are differences in the rank and grouping of those dominants which range throughout the formation. Quite a useful analogy is: *as genus is to species, so formation is to associations.*

Finally, it should be said that some ecologists and most range management scientists nowadays do accept Clements' view of the climax forest [22]. There is little doubt that his work, modified somewhat over the years, is still very important. Indeed, it is the foundation of range and forest management science in America, (see www.tarleton.edu...go to "search"and type "clements").

7 Transformations along a Sere.

Primary productivity is the rate at which energy is bound or organic material is created by photosynthesis, per unit of the earth's surface per unit time. It is most often expressed as dry organic matter in g/per square meter/year, or energy in KCal per square meter per year. Green plants are responsible for the most part for primary production and they use a portion of the organic matter they create for respiration. The total or *Gross* primary production less that amount for respiration is called the *net* primary production. For example, for a single crop, net primary productivity in grams = stems + leaves + flowers + fruits + roots + loss to insects - seeds planted.

The study of production in a natural forest is more complicated than that for a single standing crop. The reason is that there are always plants of differing ages in a forest. The techniques used by range and forest managers are called “forest dimensional analysis” and involves *allometric growth* in the form of log-log plots of diameters of trees at breast height, the trees being taken in statistically determined samples. Using tables thus constructed, one is able to estimate the dry weights of the crowns of the trees in the forest. This method was pioneered by American J. Kittredge in 1944 [28].

Letting $(x^i,\ N^i)$ denote the natural tangent bundle coordinates, consider the 2nd order system of differential equations

$$\begin{cases} dx^i/dt = k_{(i)}N^i, \text{(not summed)} \\ \\ dN^i/dt = -\Gamma^i_{jk}N^jN^k + r^i_jN^j + e^i, \end{cases} \tag{7.28}$$

where all coefficients (possibily) depend on $x^i,\ N^i,\ t$; the n^3 functions Γ^i_{jk} are homogeneous of degree zero in the N^i; and with smooth initial conditions $x^i_0,\ N^i_0,\ t_0$. For almost 20 years this system has played a major role in mathematical theories of ecology, evolution, and development in colonial invertebrates, such as corals, starfish, bryozoans and other marine fauna. The coordinates x^i are Volterra production variables, whose constant percapita rate is k_i, while the second part of this system is a description of how the different populations $N^i \geq 0$ *grow* (r^i_j), *interact* (Γ^i_{jk}) and *react* (e^i) to external influences. For our present purpose, these equations represent an *ecoscene*, the quantity x^i is *gross primary production* of modular units, like stems, leaves, flower parts, etc., for the i^{th} species. The interaction between species genererally occur among the same modular unit, i.e., roots versus roots, leaves versus leaves, etc.

ASSUMPTION *We take the term* $e^i = 0$ *in this section, representing a constant environment along the sere. Moreover, the the interaction coefficients* Γ^i_{jk} *are not explicit functions of time.*

Given a smooth scalar function $\psi(x,\ N)$, first degree homogeneous in N, then consider the transformation

$$\bar{\Gamma}^i_{jk} = \Gamma^i_{jk} + \delta^i_j\ \psi_k + \delta^i_k\ \psi_j + \dot{x}^i\ \dot{\partial}_k\psi_j, \tag{7.29}$$

where $\psi_l := \dot{\partial}_l\psi$, $\dot{\partial}_l$ indicating differentiation with respect to N^l, $x := (x^1, \ldots, x^n)$ and $N := (N^1, \ldots, N^n)$. We want to futhermore specify that, if Γ^i_{jk} are constant up to order ε^2, then $\bar{\Gamma}^i_{jk}$ are constant up to order ε^2. This obviously restricts the choice of ψ. As motivation for this definition of transformation of ecoscenes, the reader is invitated to consult the references on heterochrony [10, 11]. Moreover, consider the case $r^i_j = \lambda\ \delta^i_j$, where δ^i_j is the Kronecker delta and λ is a positive constant. Then we pass to the *long time-scale* production parameter s via $ds = \mathbf{e}^{\lambda t}\ dt$, the equations (7.28) take the 2nd order form

$$\frac{d^2x^i}{ds^2} + \Gamma^i_{jk}\ \frac{dx^j}{ds}\frac{dx^k}{ds} = 0. \tag{7.30}$$

The effect of ψ is to change the parameter s along the solutions according to

$$p = \int \mathbf{e}^{2\int \psi(u,du)}\ dt. \tag{7.31}$$

where ψ is first degree homogeneous in du, where u a dummy integration variable. The resulting 2nd order equation is

$$\frac{d^2x^i}{dp^2} + \bar{\Gamma}^i_{jk}\ \frac{dx^j}{dp}\frac{dx^k}{dp} = 0. \tag{7.32}$$

The parameter p is the new production parameter with the property that, if we set $dp = \mathbf{e}^{\bar{\lambda}t}dt$, then these equations become (7.28) with $r^i_j = \bar{\lambda}\ \delta^i_j$ and $\bar{\Gamma}^i_{jk}$ replacing Γ^i_{jk}. These are the equations for the new ecoscene. This process describes a *ecoscene transformation.*

We now can state the following theorems about *associations* and *associes*, which we assume to have, according to Clements, only a *dominant* and a *codominant.*

THEOREM A *Every 2-species ecoscene in a constant environment is transformable into any other.*

This theorem is false in every dimension bigger than 2 [35, 14].

REMARK *To secure the constant coefficients upon ecoscene transformations, it may be necessary to use different x variables,* $\bar{x} = (\bar{x}^1, \ldots, \bar{x}^n)$, *obtained by smooth non-singular transformations from the original ones. But such is by no means always necessary.*

There are special ecoscenes in our theory of transformations along a sere, among the 2-species associes.

THEOREM B *In the category of constant environments, there is a 2-species associes which is invariant under ecoscene transformations; it is necessarily classical symbiosis. Therefore, it is a 2-species association, i.e., a climax. However, the steady-state is linearly unstable.*

8 Classification of all 2-dimensional Ecoscenes.

To the data on biomass accumulation and net primary production, modern ecologists have added measurement of nutrient movements in soil, in animal harvesting of plant tissue and in leaf litter and detritus [38]. This is a philosophical move towards the view of vegetation championed first by A. G. Tansley, a British friend of Clements. This view was taken up by H. Odum in the USA and called *trophodynamics of ecosystems.* In this approach the *formation* concept is not sufficient, nor is the *biome* concept. Rather, it is necessary to include abiotic criteria and measurement. Using such information, one observes the *ecosystem* as a functional system which conserves certain of its abiotic characteristics, as well as Clementsian ones. For example, in a deciduous forest, typical nutrients include nitrogen, phosphorous, potassium, sulfur, magnesium, to name a few. These nutrients enter the plants via the root, mainly. More precisely, they enter via the symbiotic root-fungi called Mycorrhizae, which are filaments extending from the very ample root surfaces into the soil. The nutrients are more highly concentrated in the leaves than in woody tissues by a factor of 20. A reasonable quantitative statement is that nutrients in leaves occur in allometric proportions, in the same way that the leaf biomass is allometrically related to the breast high diameter of the tree [27, 28, 33].

There is an inverse relation between nutrient content and durability of plant tissues. The short-lived photosynthetic tissues, i.e., leaves, cycle these nutrients back to the soil through leaf-littering. The total amount of leaf-litter plus dead roots is in fact equal to the net primary productivity, less a small amount lost to direct animal harvesting [38]. *It follows, from the allometric relation, that the total amount of nutrients is nearly conserved. Based on this, it is now possible to postulate a formal cost of primary production in associes or associations which is conserved. Furthermore, ecoscene transformations can be defined for a class of non-constant environments which preserve the formal costs of production, in that each new ecoscene has one and it is conserved.*

We consider (7.28) again, only now we can introduce *non-constant environments* of the form

$$e^i = -\left(\delta^i_j \ \sigma_k(x)\right) \ N^j N^k, \tag{8.33}$$

where $\sigma_k(x)$ is a smooth covariant vector field on production space, where we introduce the (semi-projective) *ecoscene transformation*

$$\bar{\Gamma}^i_{jk} = \Gamma^i_{jk} + \delta^i_j \ \sigma_k, \tag{8.34}$$

so that (7.28) becomes

$$\left\{ \begin{array}{l} dx^i/dt = k_{(i)} \ N^i \\ \\ dN^i/dt = -\left(\Gamma^i_{jk} + \psi_j \ \delta^i_k + \psi_k \ \delta^i_j\right) \ N^j N^k + r^i_j \ N^j \end{array} \right. \tag{8.35}$$

where $\psi_j = \frac{1}{2}\sigma_j$. In the case $\sigma_k = \partial_k \ \sigma$ for some smooth scalar $\sigma(x)$, (8.33) takes the form

$$e^i = -\left(\partial_k \ \sigma\right) \ N^k N^i = -\frac{d\sigma}{dt} \ N^i, \tag{8.36}$$

where we have taken $k_i = 1$ for convenience. Then (8.35) reads

$$\left\{ \begin{array}{l} dx^i/dt = N^i \\ \\ dN^i/dt = -\Gamma^i_{jk} \ N^j N^k + \left(r^i_j - \delta^i_j \ d\sigma/dt\right) \ N^j, \end{array} \right. \tag{8.37}$$

which shows that a gradient-type e^i *directly affects the growth rates* of N^i.

Let us now introduce a classical notion, namely,

$$\Omega^i_{jk} := \frac{1}{2} \ \left(\bar{\Gamma}^i_{jk} - \bar{\Gamma}^i_{kj}\right), \tag{8.38}$$

the *skew-part* of $\bar{\Gamma}$, and also

$$\tau^i_{jk} := \Omega^i_{jk} - \frac{1}{n+1} \ \delta^i_j \ \Omega^a_{ak} \ + \frac{1}{n+1} \ \delta^i_k \ \Omega^a_{ja}, \tag{8.39}$$

which we call the the *Thomas tensor* of $\bar{\Gamma}$. The affine connection coefficients, Γ, $\bar{\Gamma}$ have curvatures denoted $W^i_{jkl}(\Gamma)$ and $W^i_{jkl}(\bar{\Gamma})$, respectively [10].

Let us *assume* $r^i_j = \lambda \ \delta^i_j$, $\lambda > 0$, $k_i = 1$ in (7.28). We can now state

THEOREM C *If (7.30) are Euler-Lagrange equations for* $ds = F(x, \ dx)$, *a Finsler cost functional, then a general ecoscene transformation* $\Gamma \to \bar{\Gamma}$ *results in (8.34) and (8.35), or the form,*

$$\frac{d^2x^i}{d\bar{p}^2} + \bar{\Gamma}^i_{jk} \ \frac{dx^j}{d\bar{p}} \frac{dx^k}{d\bar{p}} = 0, \tag{8.40}$$

with $d\bar{p} = \mathbf{e}^{\sigma}. \ ds$, *if and only if* $\tau^i_{jk} = 0$ *and* $W^i_{jkl}(\Gamma) = W^i_{jkl}(\bar{\Gamma})$. *In this case,* $\sigma_k = \partial_k\sigma$ *and* $\bar{F} = \mathbf{e}^{\sigma}$. *F is constant along solutions of (8.40).*

Proof. See the sections on Wagner connection theory in [16, 17, 13].

Consider now the Volterra-Hamilton system (7.28) with $e^i = 0$, $r^i_j = \lambda\ \delta^i_j$, $\lambda > 0$, and pass to the total primary production parameter s by $ds = \mathbf{e}^{\lambda\ t}\ dt$. Thus, (7.28) becomes

$$\frac{dy^i}{ds} = -\Gamma^i_{jk}\ y^j y^k, \tag{8.41}$$

where $y^i = dx^i/ds = k_{(i)}\ N^i/(ds/dt)$, and where F^2 has one of the following 3 forms:

(i) $F^2 = L^2.\ \exp\left\{2\left[-\alpha_1 x^1 + (\lambda+1)\ \alpha_2 x^2 + \nu_3 x^1 x^2\right]\right\}$, $L = (y^2)^{1+\frac{1}{\lambda}}/(y^1)^{\frac{1}{\lambda}}$, $\alpha_i > 0$;

(ii) $F^2 = (y^2)^2.\ \exp\left\{2\left[y^1/y^2 + (c_1 - c_2)\ x^1 + c_1 x^2 + \nu_3 x^1 x^2\right]\right\}$;

(iii) $F^2 = \left[(y^1)^2 + (y^2)^2\right].\ \exp\left\{2\left[\frac{\alpha_1^2+\alpha_2^2}{(\alpha_1+\alpha_2)^2}\ (\alpha_1 x^1 + \alpha_2 x^2) + \frac{\alpha_2-\alpha_1}{\alpha_1+\alpha_2}\tan^{-1}\frac{y^1}{y^2} + \psi(x)\right]\right\}$.

Here, $F = F(x, y)$ and $\psi(x) = \frac{1}{2}[\nu_1(x^1)^2 + \nu_2(x^2)^2](see[17]and[14])$.

The Euler-Lagrange equations for these 3 production cost functionals are, respectively,

(i)' $dy^1/ds + \lambda\left(\alpha_1 - \nu_3 x^2\right).\left(y^1\right)^2 = 0$

$dy^2/ds + \lambda\left(\alpha_2 + \frac{\nu_3}{\lambda+1}\ x^1\right).\left(y^2\right)^2 = 0$;

(ii)' $dy^1/ds + \left(c_1 + \nu_3 x^1\right).\left(y^2\right)^2 = 0$

$dy^2/ds + \left[\nu_3\left(x^2 - x^1\right) - c_2\right].\left(y^1\right)^2 + 2\left(c_1 + \nu_3 x^1\right).\ y^1 y^2 = 0$;

and

(iii)' $dy^1/ds + 2\ (\alpha_2 + \nu_2 x^2)\ y^1 y^2 + (\alpha_1 + \nu_1 x^1)\left(\left(y^1\right)^2 - \left(y^2\right)^2\right) = 0$

$dy^2/ds + 2\ (\alpha_1 + \nu_1 x^1)\ y^1 y^2 + (\alpha_2 + \nu_2 x^2)\left(\left(y^2\right)^2 - \left(y^1\right)^2\right) = 0$.

The Berwald-Gauss curvature scalar $\mathcal{K}$ for each case (ibid) is given as

(i)" $\mathcal{K} = \frac{\lambda^2}{\lambda+1}\ .\ \nu_3\ .\ \left(y^1/y^2\right)^{1+2/\lambda}.\ \exp\left\{-2\left[-\alpha_1 x^1 + (\lambda+1)\ x^2 + \nu_3\ x^1 x^2\right]\right\}$;

(ii)" $\mathcal{K} = 2\nu_3\ .\ \exp\left\{-2\left[\ y^1/y^2 + (c_1 - c_2)\ x^1 + c_1 x^2 + \nu_3\ x^1 x^2\right]\right\}$;

and

(iii)" $\mathcal{K} = -2\ \frac{\alpha_1^2+\alpha_2^2}{(\alpha_1+\alpha_2)^2}\ (\nu_1 + \nu_2)\ \exp\left\{\ 2\left[\phi(x) + \frac{\alpha_2-\alpha_1}{\alpha_1+\alpha_2}\ \tan^{-1}(y^1/y^2)\right]\right\}$,

where $\phi(x) = \frac{\alpha_1^2+\alpha_2^2}{(\alpha_1+\alpha_2)^2}\ (\alpha_i x^i) + \frac{1}{2}\left[\nu_1(x^1)^2 + \nu_2(x^2)^2\right]$.

We can see that the trajectories, i.e., geodesics in this case, are Jacobi stable in (i)" and (ii)", if and only if $\nu_3 > 0$. Note that $y^1/y^2 = N^1/N^2$ and $N^i > 0$. Likewise, in the case (iii)", trajectories are Jacobi stable if and only if $\nu_1 + \nu_2 < 0$.

THEOREM D (Classifications) *With* $\nu_3 = 0$ *in (i) and (ii) and* $\nu_1 = \nu_2 = 0$ *in (iii), the equations (i)', (ii)' and (iii)' give the only constant coefficients Finsler geodesics in dimension 2.*

Proof. See appendix of [13].

Let us now consider equations (7.28) with k_1 and k_2 small enough and of the same order of smallness so that *the coefficients in equations (i)', (ii)' and (iii)' are constants up to order* ε^2. Thus $k_1/k_2 = 1$ up to order ε^2, so the corresponding curvatures $\mathcal{K}$ in the 3 corresponding cases are, in general, non-vanising.

Let us now consider non-constant environment e^i of gradient type $\sigma_k = \partial_k \sigma$ with $\sigma(x) = \sigma_k x^k$. Thus, $e^1 = -\sigma_1\ (N^1)^2 - \sigma_2\ N^1 N^2$ and $e^2 = -\sigma_2\ (N^2)^2 - \sigma_1\ N^1 N^2$, and, with the pre-symbiont condition $r^i_j = \lambda \delta^i_j$, $\lambda > 0$, exactly 3 *new ecoscenes* emerge from (8.35) with Γ given by the coefficients in each of (i)', (ii)' and (iii)'. Writing only the second equation in the Volterra-Hamilton system, these are as follows:

$$\text{(i)}''' \quad dN^1/dt = \lambda\ N^1 - \tilde{\alpha}_1\ (N^1)^2 - \sigma_2\ N^1 N^2$$

$$dN^2/dt = \lambda\ N^2 - \tilde{\alpha}_2\ (N^2)2 - \sigma_1\ N^1 N^2$$

Sgn(σ_1, σ_2) is $(+,+)$ for *competition* , $(+,-)$ or $(-,+)$ for *parasitism* and $(-,-)$ for *mutualism.* All 3 cases exhibit linearly stable positive steady-states.

$$\text{(ii)}''' \quad dN^1/dt = \lambda\ N^1 - \tilde{c}_1\ (N^1)^2 - \sigma_2\ N^1 N^2$$

$$dN^2/dt = \lambda\ N^2 - \sigma_2\ (N^2)^2 + \tilde{c}_2\ (N^1)^2 - (\tilde{c}_1 + c_1)\ N^1 N^2$$

An unique linearly stable positive steady-state exists.

$$\text{(iii)}''' \quad dN^1/dt = \lambda\ N^1 - \tilde{\alpha}_1\ (N^1)^2 - \sigma_2\ N^1 N^2 + (\sigma_1 - \tilde{\alpha}_1)\ (N^2)^2$$

$$dN^2/dt = \lambda\ N^2 - \tilde{\alpha}_2\ (N^2)^2 - \sigma_1\ N^1 N^2 + (\sigma_2 - \tilde{\alpha}_2)\ (N^1)^2$$

An unique linearly stable positive steady-state exists.

Let us now pass to the total primary production parameter s in each of the above 3 systems. In the following, $dx^i/ds = y^i$:

$$\text{(A)} \quad dy^1/ds + \tilde{\alpha}_1\ (y^1)^2 + \sigma_2\ y^1 y^2 = 0$$

$$dy^2/ds + \tilde{\alpha}_2\ (y^2)^2 + \sigma_1\ y^1 y^2 = 0,$$

$$\text{(B)} \quad dy^1/ds + \tilde{c}_1\ (y^1)^2 + \sigma_2\ y^1 y^2 = 0$$

$$dy^2/ds + \sigma_2\ (y^2)^2 - \tilde{c}_2\ (y^1)^2 + (\tilde{c}_1 + c_1)\ y^1 y^2 = 0,$$

$$\text{(C)} \quad dy^1/ds + \tilde{\alpha}_1\ (y^1)^2 + \sigma_2\ y^1 y^2 + (\tilde{\alpha}_1 - \sigma_1)\ (y^2)^2 = 0$$

$$dy^2/ds + \tilde{\alpha}_2\ (y^2)^2 + \sigma_1\ y^1 y^2 + (\tilde{\alpha}_2 - \sigma_2)\ (y^1)^2 = 0.$$

The tildes over the coefficients indicate that the coefficients are approximations and constants up to order ε^2. The reason for that is the choice we made for k_1 and k_2 to be small at the same order of magnitude.

Along any solution of (A), $\mathrm{e}^{\sigma_k x^k}.\ F_i$ is constant, F_i being the Finsler function F in (i) above. Likewise, along any solution of (B), $\mathrm{e}^{\sigma_k x^k}.\ F_{ii}$ is constant, where F_{ii} is the Finsler functional in (ii) above. Simililarly, $\mathrm{e}^{\sigma_k x^k}.\ F_{iii}$ is constant along any solution of (C), F_{iii} being the cost functional in (iii) above [14].

REMARK *The reader may fairly easy verify that* $d\tilde{F}/ds = 0$ *along solutions of (A), (B), (C) where* $\tilde{F}$ *denotes the appropriate* $\mathrm{e}^{\sigma_k x^k}.\ F$ *function.*

9 Conclusion.

Of the 6 systems above, (i)', (ii)', (iii)' and $\text{(i)}^{'''}$, $\text{(ii)}^{'''}$, $\text{(iii)}^{'''}$, the $\text{(i)}^{'''}$ splits into 3 cases, namely, competition, parasitism and mutualism. Thus, there is a total of 8 systems. Each can be Jacobi stable and can exhibit linearly stable steady-states. All 8 systems have a conserved quantity, namely their associated Finsler production functionals. Yet, only the first 3 are geodesics. Moreover, all of the 8 systems model conservation of nutrients, based on our assumption that they occur in allometric proportion; nitrogen, for example, would be μx, where μ is in between 0 and 1 and x is the natural logaritm of the leaf biomass [33].

It seems to us that (ii)' or (B) above, the "commensal system", is an appropriate model for dominant/codominat forests. But as E. Warming pointed out 100 years ago, competition, parasitism and mutualism are very common in vegetative communities, so (A) or (i)' above is a model for this. Finally, (C) or (iii)' above has been used in elaborated models of coral interactions in marine ecology for more than 20 years now. It seems to us that (C) or (iii)' encodes both competition and cooperation for each modular type.

There are no conservative 2 dimensional constant coefficients Volterra-Hamilton systems with presymbiont condition other than the 8 above. All 8 are models of climax, not only with linear stability for the populations, but also stability of production, i.e., Jacobi stability. The Jacobi stability for the non-geodesic systems follows from either assuming σ_1 and σ_2 are small, or using the general KCC-theory. The computation of the curvatures $\mathcal{K}$ can be performed by the computer package Finsler [16], [34].

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