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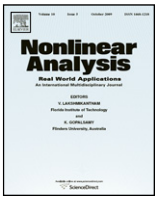

Carbon flux models in the Mata-Atlântica rain forest of Brazil

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ABSTRACT

Analytical trophodynamics (AT) here provides an ODE model of fungal fusion (FF), a popular mechanism postulated for the origin and evolution of vascular plants. The mathematics is based on the Huxley Allometric Law (HAL) in a Finsler geometry setting. Two models are presented. One, previously published, about lichens, serves as a starting point for construction of a class of stable carbon production models which exhibit HAL and model FF. These models predict that the scatter of data points around the mean for surrogates of biomass in a young tree should not be statistically greater for an older tree. Also, a parabolic cone method for tree volume estimations in the Mata Atlântica is presented. When used together with the truncated cone method, accuracy should improve, at least in some cases. Finally, production is compared for classical ecological schemes.

1. Introduction

That branch of ecology known as empirical trophodynamics (ET) is typically concerned with accumulation of biomass and the flux of energy through, say, the Mata Atlântica and is measured as forms of carbon in the traditional context of the Lindeman trophic pyramid [1,2]. However, in AT, accumulation is given by the Volterra production equations [3–5], which are as follows:

$$x^i(t) = k_{(i)} \cdot \int_0^t N^i(s)\mathrm{d}s + x^i(0), \tag{1}$$

where the $x^i(t)$ are *surrogates of biomass* (i.e., allometrically related to biomass), including secondary compounds for defense and those above listed, while N^i denotes the ith kind of *modular unit* (after J.L. Harper) such as leaves or roots [1]. The positive numbers k_i are rates and the parentheses indicate that our usual usage of the Einstein summation convention on repeated upper and lower indices is revoked for the case at hand. Thus, there is no summed term in Eq. (1).

ET addresses refinements of biomass measurements of say, carbon content of a stand of trees, and focuses on transformations between various surrogate variables, so as to investigate their flux. In AT research is centered on dynamical structures and relationships which remain invariant of the choice of any particular variable or transformation [4,5]. Such structures exist!

In addition to the above Volterra production equations, we postulate a system of ecological equations and permit their coefficients to depend on surrogates of biomass (compounds for defense, for example). This class of systems includes the classical interaction patterns of competition, mutualism, parasitism and commensalism, all of which have constant coefficients [2].

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We need an analytical definition and a symbol for *total production* which can be either gross or net production. We use $s(t)$. Since, the production process is described by the set of production variables x^i, one for each species, we can think of it as a (smooth) curve in the production space. Here, the x^i are used as local coordinates. In other words, using differential notation, we have

$$\frac{\mathrm{d}s}{\mathrm{d}t} = \left(g_{ij} \frac{\mathrm{d}x^i}{\mathrm{d}t} \frac{\mathrm{d}x^j}{\mathrm{d}t} \right)^{1/2}, \tag{2}$$

where g_{ij} is the $n \times n$ symmetric weight matrix whose entries in general depend on x^i and $k_{(i)}N^i = \mathrm{d}x^i/\mathrm{d}t$. The gross (or net) production is to be obtained by integration and is just

$$s(t) = \int_0^t \mathrm{d}s + s(0). \tag{3}$$

As an example, take

$$\mathrm{d}s = a\left(\Sigma_{i=1}^{n} (\mathrm{d}x^i)^2\right)^{1/2} = a(\delta_{ij}\mathrm{d}x^i\mathrm{d}x^j)^{1/2}, \tag{4}$$

with $g_{ij} = a\,\delta_{ij}$, a being constant times the identity matrix, where

$$a = \frac{\Sigma_i C^i}{\left(\Sigma_i (C^i)^2\right)^{1/2}}, \tag{5}$$

and m_i and x^i are Gompertz biomass and log biomass, respectively, given as $m_i = a^i \exp(-C^i \exp(-\lambda t))$, $x^i = \ln a^i - C^i \exp(-\lambda t)$ and $s = \Sigma_i x^i$ for the total log biomass. *Note that all Gompertz rates are of the same value*, λ. This is called the *Pre-Symbiont Condition*. It plays an important role in our model of endosymbiosis, later on. If we permit a non-singular change of biomass surrogates, say from x^i to $\bar{x}^i$, then (2) becomes

$$\frac{\mathrm{d}s}{\mathrm{d}t} = \left(\bar{g}_{ij} \frac{\mathrm{d}\bar{x}^i}{\mathrm{d}t} \frac{\mathrm{d}\bar{x}^j}{\mathrm{d}t} \right)^{1/2}, \tag{6}$$

where

$$\bar{g}_{ij} = g_{mn} \frac{\partial x^m}{\partial \bar{x}^i} \frac{\partial x^n}{\partial \bar{x}^j}. \tag{7}$$

We now have the symmetric weights matrix, $\bar{g}_{ij}$, depending on $\bar{x}^i$, but not of simple form (4). It is also important to realize that HAL holds in this example [6]. To see this, note first that the x^i satisfy

$$\frac{\mathrm{d}^2 x^i}{\mathrm{d}t^2} + \lambda \frac{\mathrm{d}x^i}{\mathrm{d}t} = 0, \tag{8}$$

and that, with positive initial conditions, the solutions are just (5). Then (8) are equivalent to

$$\frac{\mathrm{d}^2 x^i}{\mathrm{d}s^2} = 0, \quad i \in \{1, 2, \ldots, n\}, \tag{9}$$

whose solutions are $x^i = q^i s + p^i$ for $i = 1, 2, 3, \ldots, n$. But elimination of s from these linear equations gives HAL, the so-called linear regression of log biomass variables.

2. Comparing two production models

In the rest of this paper, we consider only two types of modular units, so $n = 2$. One type are root cells of a vascular plant and the other absorbtive hyphae of endomycorrhizal type, which penetrate the individual root cells of *tropical* trees. The fungi make an *obligate endosymbiosis* with the root cells.

We make use of the *fungal fusion hypothesis* (FF) which argues that fungi and certain photosynthetic algae joined forces eons ago and moved out of the sea and onto the land forming the very first vascular plant species [7,8]. It is widely accepted that around 90% of vascular species (tropical and non-tropical) form these *obligate* relationships. Adherents to FF see vascular land plants as complex overgrown lichens, but without any clear distinction between mycobiont and phycobiont. Such a distinction is apparent in lichens with the former a parasite on the later [2,9].

Although individual strands or filaments of hyphae are morphologically similar, there are quite distinct networks of various kinds, each serving a different role in the overall mycelium. The so-called *absorbtive hyphae* is concerned with nutrient transport up the vascular system of the tree [8,9]. We now describe the lichen model as a preliminary for the