



An entropic model of Gaia

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ABSTRACT

We modify the Tangled Nature Model of Christensen et. al. (2002) so that the agents affect the carrying capacity. This leads to a model of species-environment co-evolution where the system tends to have a larger carrying capacity with life than without. We discuss the model as an example of an entropic hierarchy and some implications for Gaia theory.

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1. Introduction

The first goal of this paper is to show how the Logistic growth model is intimately related to the Tangled Nature Model (TNM) (Christensen et al., 2002). The TNM has been extensively explored and elaborated by Jensen and others (Anderson and Jensen, 2004; Laird and Jensen, 2006, 2007; Lawson et al., 2006). The TNM was originally developed to focus on co-evolution and to study the time development of macroscopic ecological observables, such as species diversity and total population, in co-evolutionary systems. The characteristic macroscopic features of a single Tangled Nature history are long periods of stability separated by abrupt, spontaneous, transitions. These stable periods, called quasi-evolutionary stable states (q-ESS) in the literature, are characterised by a small group of symbiotic ‘core’ species which account for most of the population and a ‘cloud’ of mutants with random, positive or negative interactions with each other (Becker and Sibani, 2013). The core and cloud dynamics are crucial to understand the model and we will discuss them extensively in what follows.

In this work, we suggest a generalisation of the TNM – that the single parameter representing the carrying capacity becomes a function of the type and population of other species present in the system. We have three terms contributing to the fitness of a species a in this extended model:

- A term modelling the direct effect of individual b on a (e.g., b eats a).
- A term modelling the effect of individual b on the physical environment of a (e.g., b nests at the same sites as a).

- A term modelling an interaction between a and b whose strength is proportional to the population of b .

This third term accounts for situations in nature where the by-products of one species can have effects on other species and their ability to reproduce. This brings us to our main aim: connecting this model to ideas about life’s interaction with the earth and the body of work that is Gaia theory (Lenton, 1998; Lovelock, 1972; Lovelock and Margulis, 1974).

Gaia theory remains somewhat controversial (see e.g., Dawkins, 1983; Doolittle, 1981 or more recently Tyrrell, 2013). One part, which is more or less accepted, is that living organisms interact with and influence their inorganic environment in what can be called species-environment co-evolution. More controversial are the assertions that life maintains habitability, e.g. by acting as a thermostat to keep surface temperatures within tolerable limits. Even more controversial is the idea that life is optimising the earth to make it more habitable. The principal objections have been based on the idea that cheaters, who benefit from the improved environment without contributing, would quickly out compete the other species, collapsing the system (Free and Barton, 2007; Lenton, 1998). Our model addresses just this point: we have many individuals of different species which are more likely to reproduce if they have high fitness – given by the sum of interspecies and species-environment interactions. We find many situations where new species exploit the environment at catastrophic cost to the extant species and ultimately themselves. However we will find that, while the habitability of a single system may fluctuate up and down, across multiple systems there is a tendency for stability to increase and for life to improve habitability. We will then discuss the mechanisms causing this, which are largely entropic.

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Section 2 describes the connection between the TNM and Logistic model, and can be skipped by readers only interested in Gaia theory. We introduce our new model in Section 3, describe how we perform simulations in Section 4 and show averages across multiple histories in Section 5. Our main discussion of how the evolutionary dynamics leads to Gaia (improved stability and improved habitability as a consequence of life) is given in Section 6 and we conclude in Section 7.

2. Tangled Nature and the Logistic model

The fundamental quantity in the TNM is the reproduction probability

$$p(f_i) = \frac{1}{1 + e^{-f_i}} \quad (1)$$

a sigmoid function which takes the fitness of species i , f_i , and returns a number in $(0, 1)$ that is taken to be the probability for an individual of that species to reproduce. The TNM update step consists of choosing an individual, reproducing with this probability and then removing an individual with probability p_k (constant for all species). We set the mutation rate to 0 for simplicity, though later when we come to do TNM simulations we will have non-zero mutation rates. We can redefine $p(f_i)$ by adding a constant, A , to raise the threshold fitness below which reproduction is very unlikely (or we can imagine shifting the whole fitness landscape up or down by a constant amount)

$$p(f_i) = \frac{1}{1 + e^{-f_i + A}} \quad (2)$$

For species i , with population N_i , the average number of reproduction events is $N_i p(f_i)$ and the average number of deaths is $N_i p_k$, thus the rate of change of population of species i is roughly

$$\frac{dN_i}{dt} = N_i(p(f_i) - p_k) \quad (3)$$

For values of $f_i \approx A$ the logistic function 2 is approximately a straight line

$$p(f_i) \sim \frac{1}{2} \left(1 - \frac{A}{2} + \frac{f_i}{2} \right) \quad (4)$$

Since A is arbitrary, let $A = 2 + 4p_k$ then,

$$\frac{dN_i}{dt} \sim N_i \frac{f_i}{4} \quad (5)$$

For the TNM with the fitness function is chosen to be (Christensen et al., 2002)

$$f_i = \sum_j J_{ij} n_j - \mu N \quad (6)$$

In this and all other sums, if unspecified, the index ranges over all extant species. For simplicity we will absorb the factor $1/4$ into the definitions of J_{ij} and μ so that we are left with the equation

$$\frac{dN_i}{dt} = N_i \left(\sum_j J_{ij} n_j - \mu N \right) \quad (7)$$

for the average change in the population of N_i .

The Verhulst or Logistic growth model is much simpler. It is a differential equation

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} \right) = N_i (r_i - \mu_i N_i) \quad (8)$$

which describes a single species i , with population N_i , growing with a resource constraint. K_i is the carrying capacity, equal to the population at equilibrium $\frac{dN_i}{dt} = 0$, and the second form is a simple rewriting of the first with $\mu_i = \frac{r_i}{K_i}$.

The idea of the Tangled Nature Model, and co-evolution in general, is that the growth rate of a single species is dependent on the other species present in the ecosystem i.e., $r_i \rightarrow r_i(\vec{n})$ where

$$\vec{n}_i = \frac{N_i}{N}, \quad N = \sum_j N_j$$

We can Taylor expand r_i around the equilibrium $\vec{n} = 0$.

$$r_i(\vec{n}) = r_i(0) + \sum_j \frac{dr_i}{dn_j}(0) n_j + \dots$$

$$r_i(\vec{n}) \simeq \sum_j J_{ij} n_j \quad (9)$$

truncating at the linear term and defining $J_{ij} = \frac{dr_i}{dn_j}$. We set $r_i(0) = 0$ so that no species can grow independently of all others. This expansion is accurate when no single species makes up the majority of the population: $n_j \ll 1$ for all j . Substituting we get

$$\frac{dN_i}{dt} = N_i \left(\sum_j J_{ij} n_j - \mu_i N_i \right) \quad (10)$$

This is the Logistic growth model in the case where the growth rate is no longer intrinsic but depends the other species present in the ecosystem.

Comparing Eqs. (7) and (10) we see that the average growth rate of the TNM with no mutation and the Logistic growth model, where growth rate is a linear function of interspecies interactions, are very similar. The difference is in the damping term, μN for the TNM versus $\mu_i N_i$ for the Logistic model. In the Logistic model a species' growth is only constrained by its own population, while in the TNM a species' growth is constrained by the total number of individuals in the system. Either case may be more or less realistic depending on the ecosystem under consideration e.g., for multiple bacterial cultures growing on the same medium *in vitro* μN may be appropriate, or for an ecosystem where a single bird species competes for nesting sites $\mu_i N_i$ may be better. By considering a generalisation of the Logistic model we can allow for these two scenarios.

3. Species–environment interactions in the Tangled Nature Model

The N-species competitive Lotka-Volterra equations (see e.g., Ackland and Gallagher, 2004; Kondoh, 2003) are,

$$\frac{dN_i}{dt} = N_i \left(r_i - \sum_j \mu_{ij} N_j \right) \quad (11)$$

These equations generalise the Logistic model by making the damping term a weighted sum of the effects of each species on i . We can recover the standard TNM form by putting $\mu_{ij} = \mu$ constant or get the Logistic form by putting $\mu_{ij} = \mu_i \delta_{ij}$. μ_{ij} represents the effect of j on the carrying capacity of the system for individuals of species i .¹

Motivated by Eq. (11) we generalise the TNM fitness function to be

$$f_i = \sum_j J_{ij} n_j - \sum_j \mu_{ij} N_j \quad (12)$$

Just as we did with the growth rate we can expand the damping term as a function of \vec{n} :

¹ Eq. (11) is often written using $\mu_{ij} = \frac{r_i \alpha_{ij}}{K_i}$. We use μ_{ij} to be closer to the standard notation for the TNM.

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