

Mutual information in the Tangled Nature model

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ABSTRACT

We consider the concept of mutual information in ecological networks, and use this idea to analyse the Tangled Nature model of co-evolution. We show that this measure of correlation has two distinct behaviours depending on how we define the network in question: if we consider only the network of viable species this measure increases, whereas for the whole system it decreases. It is suggested that these are complimentary behaviours that show how ecosystems can become both more stable and better adapted.

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1. Motivation

Identifying universal features of ecosystem dynamics has been a long-standing goal in ecology. These attempts have usually involved identifying system variables that are potentially optimised during the evolution of an ecosystem. Many such candidate variables have been identified. Increasingly the focus has been on the network properties of the ecosystem, or more precisely the trophic net defined by the mass flows between the species constituting the ecosystem. However empirical evidence at the resolution needed to verify any particular claim remains out of reach for most studies. For ecologists these quantities are both of theoretical and practical interest. From a theoretical point of view it would be nice, as already noted, to find some governing principle of ecological dynamics, while practically speaking there is a need to establish a good measure of ecosystem health and maturity (Ulanowicz, 2002; Christensen, 1995).

In this paper we propose to study this issue in the context of a well established evolutionary model. The Tangled Nature model of co-evolution (Christensen et al., 2002) has already been studied in several contexts (Hall et al., 2002; Sibani and Jensen, 2005; Lawson and Jensen, 2006) and is ideal for this work as it is designed specifically to study long time behaviour in ecological networks. Its simplicity along with the rich complexity of its resulting behaviour makes it a paradigmatic model for testing co-evolutionary ideas. The model retains the binary string genotype geometry found in

previous approaches (for example the quasispecies model (Eigen and Schuster, 1977) or the NK model (Kauffman, 1990), but replaces their 'ad hoc' static fitness landscapes with a set of population dependent interactions between extant species, similar to the 'tangled' interactions of an eco-system. From a 'random' initial state, the network of extant and interacting population changes over time, slowly, but radically, enabling the system to support an ever growing number of individuals.

Despite its simplicity, the model is able to reproduce the long time decrease reported in the overall macroscopic extinction rate, the observed intermittent nature of macro-evolution, denoted punctuated equilibrium by Gould and Eldredge, the log-normal shape often observed for the Species Abundance Distributions, the power law relation often seen between area and the number of different species number, the framework of the model is also able to reproduce often reported exponential degree distributions of the network of species as well as the decreasing connectance with increasing species diversity that has attracted much observational and theoretical interest.

The details of the model are described in greater detail below, but the key aspect of its behaviour is that it moves through a series of different network configurations. In this paper we analyse these dynamic networks using tools developed in ecology. In particular, we are able to shed light on the tension between robustness and efficiency in ecological networks highlighted by Jorgensen et al. (2007). Increased correlation lead to greater brittleness in the case of perturbations, but greater robustness leads to an apparent squandering of resources. We suggest how this conflict can be resolved using evidence from Tangled Nature, where it is possible to divide the system into two interacting parts—a viable network of keystone species, and a periphery of unviable mutants. Seen

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from this perspective the apparent paradox is resolved, as the viable network becomes increasingly correlated, while the total network (including many species *in potentia*) develops greater redundancy.

2. Review of the basic behaviour of the model

2.1. Type space and the interaction matrix

A type is represented by a vector S of L elements belonging to the set $[0, 1]$. Thus there are 2^L possible types, corresponding to the vertices of a unit hypercube in L -dimensions. S may be interpreted as a genome, or a set of characteristics—either way it is directly susceptible to mutations and defines the type completely (that is there is no phenotype level in this model). Each type, which we can index by a number i in the range 1 to 2^L to simplify notation, has a population of $n_i(t)$ identical individuals, so the total population is the sum over all the 2^L possible types

$$N(t) = \sum_{i=1}^{2^L} n_i(t) \tag{2.1}$$

The ability of an individual to reproduce is determined by how it interacts with the other types present at a given time. This is formalised in the reproduction weight function (which is then turned into a probability of reproducing—see below)

$$H_i(t) = \frac{C}{N(t)} \sum_{i=1}^{2^L} J(S_i, S) n(S_i, t) - \mu N \tag{2.2}$$

where the sum is over all other types, C is a control parameter that determines the level of inhomogeneity in the population, $N(t)$ is the total population at time t , and $n(S, t)$ is the population of type S .

Two types S_i and S_j are coupled via the interaction matrix $J(S_i, S_j)$ that can be either positive negative or zero. This number is intended to be the sum of all the influences of i upon j . This interaction matrix is unrelated to the type space outlined above so there are no correlations in the interactions between different types—that is $(J(S_i, S_j)J(S_k, S_j)) = 0$ even if the average is restricted to neighbours in type space. This interaction is not necessarily material in nature but may represent any influence that one type has on another. The overall connectivity of the interaction matrix is set by a parameter Θ which for this paper has a value of 0.2 (that is 0.2 of all possible connections between types actually exist). The distribution of the nonzero values of the function $J(S_i, S_j)$ are irrelevant as long as they are distributed in some reasonable, continuous way. The interaction matrix is constructed such that if $J(S_i, S_j)$ is nonzero then $J(S_j, S_i)$ is also nonzero. This means there are three types of interaction—mutualistic, antagonistic and predator–prey. Fig. 1 illustrates the key components of the tangled nature model—the hypercubic type space, varying type occupancies, and the different types of possible interaction between types.

2.2. Reproduction, mutations and death

The model is simulated stochastically, with a time-step consisting of the following: one individual is selected at random, and reproduces asexually according to the probability

$$Pr(S_i, t) = \frac{1}{1 + \exp[H(S_i, t)]} \in [0, 1] \tag{2.3}$$

If successful the individual is replaced with two copies. In each of these copies there is a probability of mutation per ‘gene’, p_m . Another individual is picked at random and is killed with probability p_k .

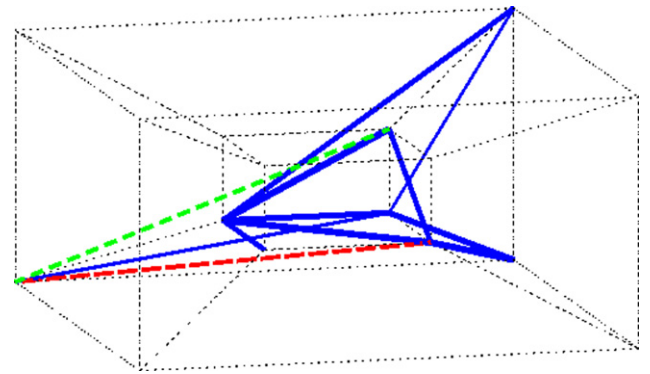


Fig. 1. An example of the configuration of the Tangled Nature system in a meta-stable state. This is a four dimensional model for expository purposes only, the model in this paper has 20 dimensions. The vertices of the hypercube represent the 16 possible types in the model. The dotted lines represent nearest neighbour links in type space, and the solid lines represent non-zero interaction terms with blue = black solid, red = dashed in front, green = dashed behind (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

2.3. General behaviour of the model

We start a run with $N(0) = 1000$ individuals on one randomly chosen site. Initially there is no reproduction, since there can be no interactions between species, so H is very negative and the probability of reproduction is zero. Then as the resource limitation term diminishes, reproduction becomes possible, and consequently some new types are generated by mutations. Once interactions between these new types begin, the interaction term in the reproduction probability becomes significant. After some re-organisation, a set of species that interact in a stable way emerges, and persists for some time (see Fig. 2). This period of stability is ended by another chaotic reorganisation, from which another meta-stable state emerges.

The bulk properties of these meta-stable states turn out to depend on the age of the system—the system slowly optimises the interactions between species, as evidenced for example by the logarithmically increasing population (Fig. 3). It is this non-stationary aspect of the model that this paper tries to explain, albeit only partially.

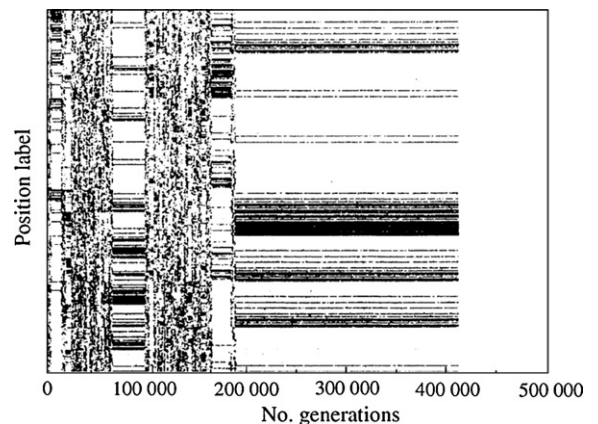


Fig. 2. Overview of a typical run of TaNa. The y-axis is simply a species label, ranging from 1 to 2^L , and the x-axis is time in generations. If a position is occupied at a given time, a dot is placed at the corresponding number for that time step. The plot clearly shows the alternating stable and unstable periods. The stable periods are characterised by a steady population and constant set of species, whereas the transitions have a constantly changing set of species (e.g. between 100,000 and 150,000 generations). Figure from Christensen et al. (2002).

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