ECOLOGICAL COMPLEXITY 3 (2006) 253–262

available at www.sciencedirect.com

journal homepage: http://www.elsevier.com/locate/ecocom

The Tangled Nature model with inheritance and constraint: Evolutionary ecology restricted by a conserved resource

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ARTICLE INFO

Article history:
Received 1 November 2005
Received in revised form
2 June 2006
Accepted 3 June 2006
Published on line 18 July 2006

Keywords:
Evolutionary ecology
Resource constraint
Bio-diversity
Species lifetimes
Connectance
Species degree distribution

ABSTRACT

We study a version of the Tangled Nature model of evolutionary ecology redefined in a phenotype space where mutants have properties correlated to their parents. The model has individual-based dynamics whilst incorporating species scale competitive constraints and a system scale resource constraint. Multiple species arise that coexist in a species interaction network with evolving global properties. Both the mean interaction strength and the network connectance increase relative to the null system as mutualism becomes more extensive. From a study of the dependence of average degree on the resource level we extract the diversity-connectance relationship which conforms to the hyperbolic form seen in field data.

This is adjudged to arise as a consequence of the evolutionary pressure to achieve positive interactions. The network degree distributions conform more strongly to exponential than to the null binomial distributions in all cases. This effect is believed to be caused by correlations in the reproductive process. We also study how resource availability influences the phenotypical lifetime distribution which is approximately of power law form. We observe that the mean lifetime is inversely related to the resource level.

1. Introduction

A functioning ecosystem relies on various environmental resources to sustain its component species with some of these resources being universally required for survival. The limitation of supply rate or overall quantity of such a resource, acts as a restriction to the development of an ecosystem and systematic properties are expected to depend on the level at which this occurs (Loeuille and Loreau, 2003). It is known from field data that the diversity of species changes across energy and water gradients such as is found in latitudinal variations (Hawkins et al., 2003; Bonn et al., 2004). In general, large scale heterogeneous environments will support greater species numbers at higher resource availabilities with the relationship taking a monotonically increasing form (Currie, 1991; Waide et al., 1999; Bonn et al., 2004). At smaller scales this relationship takes a uni-modal form as competition effects between species elevate with increasing productivity.

Any changes in diversity combined with knock-on effects of competition could conceivably lead to a change in the topology and dynamics of the species interaction network. These networks and their associated interaction matrices have been studied and are considered to be significant in adjudging the stability and permanence of ecosystems (May, 1974; Tregonning and Roberts, 1979).

There has been a great deal of research investigating the short term effects of resource variation on ecosystems (Tilman, 1982; Hulot et al., 2000), but very little on the impact of resource levels over evolutionary timescales. Also, recent work has focused on the dynamical coevolution of species

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doi:10.1016/j.ecocom.2006.06.001

populations (Tokita and Yasutomi, 2003; Drossel et al., 2004; McKane, 2004; Coppex et al., 2004) but these approaches use continuum descriptions whilst evolution occurs via dynamics associated with discrete individuals. To address these issues accordingly we present a model of evolutionary ecology that functions at the level of the individual whilst incorporating species scale competitive constraints and a system scale resource constraint.

In the uncorrelated version of the Tangled Nature model a spatially distributed system was investigated and diversity scaling was found to occur with the variation of system size (Lawson and Jensen, 2005). The present model though is intended to represent ecosystem dynamics where members are localised and in reasonable proximity to one another. As a result spatial aspects are not considered when determining the functional form of the interactions. No specific scale is set here and we define an ecosystem simply through localisation. If two system members have phenotype descriptions such that they are deemed able to interact then they will interact. One property though is imposed upon the system by virtue of the inclusion of intraspecific competition effects. We assume that the system is heterogeneous thus allowing diversity to occur through implied specialisations. Niches are not explicitly considered but the system can be perceived as being environmentally diverse so permitting multiple phenotypes to occur concurrently without continual competitive exclusion. The conserved resource limits the system as a whole but identical or sufficiently similar phenotypes will also be limited by intraspecific competition.

Our work follows from the Tangled Nature model of evolutionary ecology (Christensen et al., 2002; Hall et al., 2002; Collobiano et al., 2003; Anderson and Jensen, 2005), which demonstrated species formation as a result of individual-based dynamics. These species were then studied in terms of their interaction networks and other more dynamical features such as extinctions, lifetimes and stabilities. Recently, the model was simplified by restricting the reproductive process to non-overlapping generations (Rikvold and Zia, 2003; Zia and Rikvold, 2004). This allowed both longer timescales to be simulated and a deeper analytical treatment to be made available. Modifications made to the description of individuals have now allowed us to include a gradual species evolution within a significantly larger *phenotype* space. Correlations introduced into the structure of this space mean that inheritance from parent to mutated offspring is available and also mathematically quantifiable which was not the case in the previous model. Attempts have been made to impose correlations onto the hypercubic genotype structure of the earlier model (Sevim and Rikvold, 2005) but with only limited effect. Here we use a different procedure to construct a correlated phenotype space which allows us to consider much larger spaces. We find that correlations in these huge phenotype spaces have a significant effect.

Our paper is arranged as follows. In the first part of Section 2, we describe how the system members are represented in terms of a hypothetical phenotype space. This representation is used to provide a fully determined, correlated interaction-space. As the processes involved in this are somewhat laborious we have consigned the wider details to Appendix A, whilst giving an overview in the main text. In the second part of Section 2, we describe the update rules for the system and how the reproductive probabilities are determined from the species interaction network. We approach the dynamical evolution in a stochastic discrete manner as we see it as appropriate for a discrete-entity system such as this. Statistical fluctuations are important as population numbers may become low and coupled dynamics across an interaction network could be heavily dependent upon them.

Results regarding the issues of diversity, lifetime distributions and network properties are presented in Section 3, and a discussion of these along with future directions are set out in Section 4.

2. Model

2.1. Interactions

Individuals are represented by vectors, $\mathbf{T}^{\alpha} = (T_1^{\alpha}, T_2^{\alpha}, \ldots, T_L^{\alpha})$, in a phenotype space of dimension $L = 16$, with specific individuals denoted by Greek lettering α, β, $\ldots = 1, 2, \ldots N(t)$, where $N(t)$ is the population at time, t. Each trait T_i^{α} may take an integer coordinate in the range [0; 99,999] that is periodically bounded allowing the points $T_i^{\alpha} = 0$ and $T_i^{\alpha} = 99,999$ to be contiguous. The phenotype coordinates themselves are arbitrary and are not intended to represent any kind of quantitative scale so the periodic boundary is introduced to maintain their arbitrariness. Traits are not assigned any qualities nor properties; they are simply descriptions used for determining distinct phenotypes and therefore distinct pairwise interactions. The periodic boundary prevents any occurrence of bias due to edge effects as the evolution shifts the distribution in phenotype space. As the space is large the possibility of circumnavigating this periodicity is very small. The large integer range is used to emulate the continuous nature of many real organism traits and as a result the extant phenotypes are capable of gradual adaptation during the evolutionary process.

The co-evolution of the extant phenotypes is primarily controlled by the interactions they have with one another. These are represented by $\mathbf{J}(\mathbf{T}^{\alpha}, \mathbf{T}^{\beta})$, the interaction strength effected upon α by β, which is independent of $\mathbf{J}(\mathbf{T}^{\beta}, \mathbf{T}^{\alpha})$. As the phenotype space is a closed set of $100000^{16} = 10^{80}$ possible states the interaction space is a closed set of $10^{80} \times 10^{80} = 10^{160}$ possible pairwise interactions that exist in potentia. This set of all possible phenotype interactions is constructed with the property that only a subset of them are non-zero quantities. This proportion or connectance, θ_0 is defined at the outset and represents the fact that a specified phenotype will interact only with a subset of all other conceivable phenotypes. The resulting set of non-zero interactions are assigned strength values that are normally distributed.

A system created with a random group of phenotypes will, on average, conform to the above properties (i.e. connectance, $\theta = \theta_0$, plus interaction strengths that are normally distributed). But, once the evolutionary process is underway the phenotypes existing at later times may have interaction properties that deviate from those of the random null system. The fact that we pre-define the properties of the closed interaction