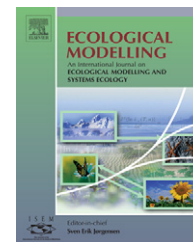


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# On the use of multi-species NK models to explore ecosystem development

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## ABSTRACT

The search for general laws governing the co-evolution of ecological communities, and the resulting trends in the development of ecosystem structure has led researchers down at least three broad paths, exploring: (1) thermodynamics, (2) networks, and (3) species assemblages. Recently, Fath and Grant [Fath, B.D., Grant, W.E., 2007. Ecosystems as evolutionary complex systems: network analysis of fitness models. *Environmental Modelling & Software* 22, 693–700] suggested the possibility of linking ecological network analysis to multi-species NK models of self-organizing systems [Kauffman, S.A., 1993. *The Origins of Order: Self-organization and Selection in Evolution*. Oxford University Press, Oxford, 709p.] to explore the dynamics of ecosystem development. In this paper, we describe modifications to the multi-species NK model that allow connectedness among species, or ecosystem structure, to evolve during a simulation, examine the robustness of model behavior to changes in the number of both species and genes included in the system, and use the modified model to simulate ecosystem development over 200 generations for each of 23 combinations of number of species and number of genes in the system. Simulated system connectedness evolved noticeably and quickly to an intermediate, but lower than expected, level as a consequence of system self-organizational processes strong enough to override the random processes at work in the system, and general trends in relative system connectedness were robust to changes in the number of species and the number of genes included in the system. We compare these trends in system connectivity to those generated by the Tangled Nature model [Laird, S., Jensen, H.J., 2007. Correlation, selection and the evolution of species networks. *Ecological Modelling* 209, 149–156] and to those based on field data on food webs, and comment on future work using multi-species NK models to explore ecosystem development.

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## 1. Introduction

The overwhelming complexity of nature has fascinated and bewildered us since the beginning of time. Great advances in our understanding of nature have resulted from ingenious (and heroic) simplifications of this complexity, some of

which we know as the basic laws of geometry, physics, chemistry, and thermodynamics. But we lack equally basic laws of biological co-evolution. Certainly, we have useful simplifications of the mechanics of biological evolution (population genetics) and the functioning of pair-wise ecological interactions (competition, predation, parasitism, and mutualism),

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which we extend, with rapidly diminishing confidence, to very small assemblages of species. We also have simple indices that we commonly use to track changes in ecosystem structure and function (species diversity, standing crop biomass, and net biomass production), and Odum (1969, Table 1) long ago hypothesized 24 qualitative trends in community structure, energetics, nutrient cycling, and overall homeostasis that should be expected during ecosystem development. But the search for general laws governing the co-evolution of ecological communities, and the resulting trends in the development of ecosystem structure, continues (Lawton, 1999; Jørgensen and Fath, 2004).

This search has led researchers down at least three broad paths, exploring: (1) thermodynamics, (2) networks, and (3) species assemblages. Some have viewed ecosystems as thermodynamic, dissipative structures, seeking general laws governing trends in thermodynamic efficiencies of the system as a whole during ecosystem development (Mejer and Jørgensen, 1979; Aoki, 1987, 1988; Müller and Leupelt, 1998; Jørgensen, 2002; Fath et al., 2004). Others have viewed ecosystems as structural networks of interconnected species, seeking general laws governing trends in the information content of the system as a whole inherent in the connections among species (Patten et al., 1976; Ulanowicz, 1986; Higashi and Burns, 1991; Patten, 1998; Fath and Patten, 1999; Fath et al., 2001; Fath, 2004). Still others have viewed ecosystems as assemblages of large numbers of individual organisms or species, seeking general laws governing trends in speciation, extinction, and species diversity (Kauffman, 1993; Christensen et al., 2002; Hall et al., 2002; di Collobiano et al., 2003; Newman and Palmer, 2003). Clearly, these approaches differ with regard to specific objectives, all have their merits, and cross-fertilization should prove fruitful. For example, Nielsen and Ulanowicz (2000), while exploring the compatibility of the thermodynamic and structural network approaches, found that changes to ecosystems that augmented the information content of the system as a whole also increased thermodynamic efficiency.

Here, we focus on the use of individual-based, self-organizing models to explore structural changes in species connectivity networks during ecosystem development. The general idea is to use multi-species NK models (described below) to simulate the “co-evolution” of species connectivity networks of the type used to calculate ecological goal functions via network environ analysis. Historically, quantitative investigation of the behavior of ecological goal functions has been based primarily on static or equilibrium analyses of small highly aggregated systems (Jørgensen, 2002; Müller and Leupelt, 1998). Recently, Fath et al. (2004) investigated the directional change of ecological goal functions during four characteristic stages of development, but the impetus of change was not addressed. This left unanswered the important question of how these networks evolve over time. Fath and Grant (2007) suggested the possibility of linking network environ analysis to dynamic multi-species NK models of self-organizing systems (Kauffman, 1993) as a way to address this gap. That is, we could use multi-species NK models to investigate the impact of evolving structural network properties on the functional thermodynamics of the system.

In this paper, we describe some modifications to the multi-species NK model that remove unnecessary restrictions on changes in system connectivity, and examine the robustness of model behavior to changes in the number of both species and genes included in the model. We then comment on how the evolving degree and pattern of connectedness among species generated by the model might be used to explore trends in ecosystem development. Our goal is to develop a simple, completely general model that focuses attention on the self-organization of connectedness in complex systems, in the absence of ecological restrictions imposed by energy limitation or the particular details of species interactions. This simple model, in which ecosystem development proceed based only on randomly generated local variations in fitness, will provide the basis for future ecological extensions exploring commonalities in the thermodynamic, network, and species assemblages approaches to studying ecosystem development.

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## 2. The NK model

NK models are analogous to the family of spin-glass models used in statistical physics (Edwards and Anderson, 1975; Derrida, 1981). NK models, or modifications thereof, have been used to explore properties of adaptive evolution (Kauffman and Levin, 1987), molecular and genomic evolution (Kauffman and Weinberger, 1989; Cooper and Podlich, 2002), self-organization in biological systems (Kauffman and Johnsen, 1991; Kauffman, 1993), extinction (Newman and Palmer, 2003), and over the last decade have been applied to modeling strategies in business and management (Levinthal, 1997; Solow and Leenawong, 2003). NK models have not been used widely in ecosystem ecology, most likely because of the conspicuous absence of specific ecological structures (e.g., trophic levels) and ecological processes (e.g., competition and predation). However, this very lack of specific ecological constraints provides an ideal, “ecologically null” model of a self-organizing, complex system. The corresponding null hypothesis is that the specific characteristics of ecological systems are unimportant in terms of affecting general trends in system development.

Details of the basic NK model are available elsewhere (Kauffman and Levin, 1987; Kauffman and Weinberger, 1989; Kauffman and Johnsen, 1991; Kauffman, 1993, 1995, 2000), thus we provide only a brief summary here. The basic module represents an organism with  $N$  genes, each having two alleles, 0 and 1. The contribution of each gene to the fitness of the individual depends on the allele of that gene and the alleles of  $K$  other “epistatic” genes in its genome. Each allele is randomly assigned a fitness contribution value between 0.0 and 1.0 for each of the  $2^N$  combinations in which it occurs. The overall fitness of each combination of alleles, that is, of each genotype, is equal to the mean of the fitness values of the constituent alleles. Thus each genotype has a specific fitness value between 0.0 and 1.0, and, collectively, the set of fitness values of all possible genotypes forms a “fitness landscape” for that individual, which is assumed to represent the fitness landscape for the entire species (each species

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