

Diversity as a product of inter-specific interactions

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Abstract

We demonstrate diversification rather than optimization for highly interacting organisms in a well-mixed biological system by means of a simple model of coevolution. We find the cause to be the complex network of interactions formed, allowing species that are less well adapted to an environment to succeed, instead of the ‘best’ species. This diversification can be considered as the construction of many coevolutionary niches by the network of interactions between species. The model predictions are discussed in relation to experimental work on dense communities of the bacteria *Escherichia coli*, which may coexist with their own mutants under certain conditions. We find that diversification only occurs above a certain threshold interaction strength, below which competitive exclusion occurs.

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1. Introduction

Understanding how diversity arises through evolution and is sustained in an ecosystem is an important issue. One of the key questions therein is whether interactions between organisms enhance or suppress diversity. If there is no explicit symbiotic interaction, it would be expected that the competition for a given resource leads to exclusion of many types. This results in monodominance, i.e. the survival of the fittest, as determined by Gause’s competitive exclusion principle (Gause, 1934). In contrast, in the presence of strong interactions, diversification has been shown to occur both in numerous models and in experiment (Helling et al., 1987; Czárán et al., 2002). We attempt to understand the relationship between interaction and diversity at a general level, and will relate our work to experimental findings on evolution in *Escherichia coli* (Kashiwagi et al., 2001).

We show that the diversification can indeed be facilitated by the interaction, using a range of different fitness concepts. We do this by adopting a slightly modified version of the Tangled Nature (TaNa) model (Christensen

et al., 2002; di Collobiano et al., 2003; Hall et al., 2002). In addition to the standard inter-specific interaction in the TaNa model, we allow types to differ in ‘intrinsic fitness’—the fitness of a type in the environment, in the absence of other types. A self-supporting, dominant genotype may coexist with, or be displaced by, a number of other genotypes that are less efficient competitors for the resource individually, provided that strong enough interactions are permitted. Diversity is maintained via the complex network of interactions, and we demonstrate a cutoff interaction strength below which monodominance persists. We split the ‘intrinsic fitness’ of a type into *density dependent* (i.e. the interaction with own type) and *density independent* parts, and study them separately. The conditions on the interaction strength are, respectively: (1) the net positive interaction with *other* types is greater than the *density-dependent* fitness, (2) the net positive interaction with other types is greater than the *density-independent* fitness *difference* between types.

The idea that diverse states can be supported by interaction is not new. Gause’s competitive exclusion principle states, in the general case (Dieckmann et al., 2003), that ‘the dimension of the environmental interaction variable is an upper bound for the number of species that can generically exist at steady state’. Although

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environmental interactions cannot in general be uniquely identified, and so this dimension is not known, it is still possible to support high diversities robustly (Tokita and Yasutomi, 2003; Meszéna et al., 2006) (i.e. still supported with a small change in the environmental parameters). This diversity remains finite even in the case of an infinite environment interaction variable (Gyllenberg, 2005), as species must be ‘different enough’ (MacArthur and Levins, 1967) to coexist stably. In addition, a greater number of species than environmental factors may be supported by oscillations or chaos, e.g. Vandermeer et al. (2002), Huisman and Weissing (1999), and Kaneko and Ikegami (1992). The appearance of diversity in a system with strong interaction is therefore not a surprise by itself, as each interaction contributes to the effective dimensionality. Still, it is important to understand how diversity is mediated by the interaction.

We follow May (1973) in using generalized, random interactions. In his book he discusses the ecological implications of such models in detail; we will be looking at the effects of evolution on that stability. Such simple models may most accurately describe molecular replicators (e.g. Eigen et al., 1988), and simple bacterial systems. However, because only the net interaction and reproduction probability is considered, there are other biological cases which can be approximated by this approach.

Our model is individual-based without any individual aging, considering a generalized system of organisms so that interactions are random. Genotype space is pre-defined, so that the interactions between all possible organisms are fixed from the start, and mutations are local. In the spirit of other null models, these interactions are not correlated in this version of the model. We consider one reproduction attempt as the basic unit of time, and we allow mutation to occur during the population dynamics. The total population is a result of the dynamics. We will consider an intrinsic fitness landscape in the presence of strong interactions. For general background reading on individual-based modelling and for discussion on many basic features the reader is referred to Drossel (2001), to Droz and Pękaliski (2004) for a population dynamics perspective, and Pigliucci and Schlichting (1997) for a genetics point of view.

The features described above mean that the existence of diversity can be seen to arise in the following way: from an initially monodominant state we find that evolution forces a search of genotype space for the most stable configurations. Often these states are diverse, provided the intra-specific competition exceeds inter-specific competition (or, equivalently, the beneficial inter-specific interaction is greater than the intrinsic fitness). Such diverse states do not exist for low interaction strength, and all states are diverse in the limit of very high interaction strength. Stability is determined by the properties of a given configuration in genotype space, and states are, on average, more stable as time progresses. In addition, we find a sharp

threshold in interaction strength below which diversity does not occur.

2. Definition of the model

We now define the TaNa model. Individuals are represented as a vector $\mathbf{S}^\alpha = (S_1^\alpha, S_2^\alpha, \dots, S_L^\alpha)$ in genotype space \mathcal{S} . The S_i^α take the values ± 1 , and we use $L = 20$ throughout, giving $2^{20} = 1\,048\,576$ possible types. Each \mathbf{S} string represents an entire type with unique, uncorrelated interactions. The small value of L is necessary for computational reasons as all types exist in potentia and have a designated interaction with all other types.¹ There are therefore $(2^{20})^2$ interactions to be considered in this model. We consider random interactions for simplicity, which would be correlated in reality. Introducing significant correlation whilst maintaining randomness in this relatively small hypercubic genotype space has proved difficult, and so we consider uncorrelated interactions here. Note that controlled correlations have been achieved in another version of the model (Laird and Jensen, 2006).

We refer to individuals by Greek letters $\alpha, \beta, \dots, = 1, 2, \dots, N(t)$. Points in genotype space are referred to as $\mathbf{S}^a, \mathbf{S}^b, \dots$, and any number of individuals may belong to a point in genotype space \mathbf{S}^a .

In the original TaNa model, individuals α are chosen randomly and allowed to reproduce with probability p_{off} :

$$p_{off}(\mathbf{S}^\alpha, t) = \frac{\exp[H(\mathbf{S}^\alpha, t)]}{1 + \exp[H(\mathbf{S}^\alpha, t)]} \in (0, 1). \quad (1)$$

They are then killed with probability p_{kill} , which is a constant parameter. The difference between the original model and the one used here is the definition of the weight function $H(\mathbf{S}^\alpha, t)$. The original version used was

$$H_0(\mathbf{S}^\alpha, t) = \frac{k}{N(t)} \sum_{\mathbf{S} \in \mathcal{S}} J(\mathbf{S}^\alpha, \mathbf{S}) n(\mathbf{S}, t) - \mu N(t). \quad (2)$$

Here k ($\equiv 1/c$ from previous papers) determines the maximum strength of interactions, $N(t)$ is the total number of individuals at time t , and $n(\mathbf{S}, t)$ is the number of individuals with genotype \mathbf{S} at that time. The *interaction matrix* $J(\mathbf{S}^\alpha, \mathbf{S})$ represents all possible couplings between all genotypes, with $J_{ii} = 0$ always and $J_{ij} = J_{ji} = 0$ with probability Θ . If the interaction is not zero, then J_{ij} and J_{ji} are both generated randomly in the range $(-1, 1)$, so that mutualism, predator–prey, and competition are all possible, but amensalism and commensalism only occur in

¹When discussing the model, we refer to points in genotype space as a type. It is a matter of interpretation whether we consider genotype space to be ‘coarse-grained’ (resulting in each genotype being a different species—valid when k and ε are ‘large’ so that genotype differences affect reproduction probability greatly; see Eq. (2) for definitions), or whether we consider genotype space to be a small sample of a much larger space, meaning genotypes are *types* of a base species (which would be valid when k and ε are small, and so all genotypes have similar reproduction probabilities). As we operate in neither extreme and reproduction is asexual, the distinction between species and type is difficult.

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