

# Sustained Evolution from Changing Interaction

George Kampis<sup>1</sup> and Laszlo Gulyas<sup>2</sup>

<sup>1</sup>Department of History and Philosophy of Science, Eötvös University, Budapest

<sup>2</sup>Computer and Automation Research Institute, Hungarian Academy of Science  
gk@hps.elte.hu

## Abstract

We develop and analyze an agent-based simulation model the purpose of which is to achieve sustained evolution under sympatric conditions. Evolution is understood in the form of speciation, i.e. the emergence of reproductively isolated and functionally distinct populations. In the model, reproduction is expressed as a function of phenotype to phenotype interaction. A population with a given set of phenotypic interactions tends to adaptive stasis, whereas if the interaction space changes, so that new dimensions are added in the course of the process, new species can emerge. We show that this behavior is stable and leads to a persistent production of new species.

## Introduction

Sustained evolution is a notorious problem of evolutionary simulations (Bedau et al. 2000, Brooks 2001, Standish 2002, Holland 2003) as well as of fundamental theory (Stenseth and Maynard Smith 1984). In particular, species emergence is difficult to achieve without the artificial introduction of reproductive barriers (such as allopatric conditions).

Motivated in part by niche construction (Laland et al. 2000), exaptation (Gould and Vrba 1982), and studies of causality (Kampis 2003), we develop a model of species emergence based on phenotypic interactions. The key ingredient of the model is the updating of selection forces that arise from phenotype to phenotype interaction change, implemented here as a dimensionality increase of the interaction space.

## Theory

Evolutionary simulations tend to 'run out of steam' as a result of the very adaptation process defined by the selection forces. Adaptation is akin to optimization: when optima are approached, little room is left for further development. In order to proceed towards open-ended, free evolution, the task of the evolution process needs to be redefined 'on the fly'. This recognition is present in various forms in biological evolution theory, e.g. niche construction and related concepts (Lewontin 1983, Odling-Smee et al. 2003). The idea explored in this paper comes from the study of natural causation (Kampis 2002a,b). Causal interactions are 'fat', i.e. they occur in parallel, and invoke many simultaneous levels and variables. A real-world evolution process of genetic 'replicators' is always built upon the underlying phenotype-to-phenotype interaction of

individuals as 'interactors'. If the process is modeled at the interactor level, effects of 'fat' causal interactions should be taken into account. These effects can induce new evolutionary change from the relational flexibility of 'fat' phenotype (Kampis and Gulyas 2003).

The basic concept here is that of *interaction space*. The interaction space defines how phenotypes 'see' each other, and is itself an evolutionary product. As a consequence, phenotypes are less rigidly defined than genotypes. This is easily understood in a simple example such as sexual selection. What is a relevant variable when pairing two organisms is, in the one individual, a matter of the other individual's interacting variables. Mating occurs, roughly speaking, if the two sets of variables fit, e.g. when the female prefers male antlers (variable 1) and the male possesses such antlers (variable 2). Then, a fit, or match, is possible, and reproduction will occur, which propagates both the genotypes and the phenotypes. Such a match is "groundless", however – it is based on nothing but the relational properties of the two phenotypes.

This characteristic of sexual selection is, we suggest, a suitable metaphor for more general ecological and evolutionary interactions. The idea is that interaction space can radically change with little or no genetic component. Once changed, however, it has dramatic effects on differential survival, leading to major genetic change.

The current simulation we present is confined to the case of sexual selection. To test the theory, we demonstrate that in a sexual selection-based species, evolution can transform and eventually split a population if individuals with a new phenotype which redefines interactions (such as a female that prefers body size instead of antlers) are produced.

It is important to understand how interaction space works. With the introduction of 'dissenter' individuals having a new interaction component, silent phenotype traits of every other individual (i.e. their body size, in the given example) become suddenly highlighted, and become part of a changed ecological interaction space. Every individual is effected by such a transition, as they are all potential mating partners of the dissenter(s); some preferred, some not. Not affected by prior selection, such phenotypic properties can vary more widely along the new dimension. As a result, the old sexual selection pressure becomes supplemented by a new one, arising spontaneously and endogenously, within a fully sympatric population. Next, new sexual selection can lead to the development of a new best match, and to a novel, sexually reproducing, stable sub-population, reproductively isolated from the original.

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## The Model

We study sexually reproducing gender-less (i.e. 'snail-like') agents, hereafter called organisms or individuals. Reproductive success depends on a similarity metric which introduces sexual selection. Genotypes and phenotypes are assumed to coincide; however, the model's behavior is based on a phenotype interpretation. Individuals are represented as parameter vectors in phenotype space. In the current version of the simulation, the only internally (i.e. in the course of a run) adjustable parameters are the phenotype vectors. The evolutionary process is an outcome of the pairing of phenotypes for reproduction. Any two organisms will reproduce if they ever meet and if they are sufficiently similar. Depending on the degree of similarity, more or less offspring will be produced. This selection force is variable (any individual can become the 'center' of a species) yet well defined (once a center is formed, distant individuals are selected against). A species is a dynamically maintained cluster of interbreeding individuals around an emergent center, characterized by the property vector of its dominant types.

### Interaction change

Interaction change is represented in the model as the change of the dimensionality of the phenotype vector at the birth of a new 'dissenter' agent. The transformation of dimensionality introduced in one individual globally redefines interaction space, as it is instantaneously 'felt' across the whole population, as reflected in the global nature of the concept of interaction space. For simplicity, we will only study effects of dimension increase. This corresponds to the situation where the introduction of a new interaction, such as when paying attention to a newly defined sexual trait in mating, does not imply the neglect of the previously favored traits.

Once this general framework is specified, the key question of the model is to allocate new phenotype values to the new interaction dimension. In accordance with the theoretical considerations mentioned, we allow new values to be 'stretched' along the new dimension, which increases variance. For this so-called 'new dimension' procedure, we implemented two different, arbitrary methods. We studied type-independent and type-based methods. The latter assign identical values to identical phenotypes, the former don't.

### The evolution engine

Experiments were conducted using a basic evolution engine, the task of which was to maintain a stable population before we develop new species. The evolution engine was written using an agent-based approach, in the REPAST environment developed by the University of Chicago (Repast 2003). The engine defines the usual evolutionary background, complete with reproduction, mutation, crossing over, aging, and death. It provides a 'sympatric' (i.e. panmictic) environment without a spatial component. With this engine, we simulate a partial artificial

ecology that has one resource, namely, energy. Each organism has an equal chance to 'eat' in every time-step. Note that this already introduces an implicit competition for energy, which leads to density-dependent effects: genotypes represented with a higher number of individuals obtain a larger share. Reproduction is implemented similarly. More abundant genotypes have more offspring on the average, even if reproduction rates are equal. This yields a higher-than-linear growth, i.e. 'hypercompetition', a phenomenon typical for many evolution models.

The evolution engine, left alone, maintains a single species under a very wide range of parameters. We applied conditions where a constant energy influx constrains the maximum average number of individuals. That is, new species can only emerge at the indirect cost of others, as the overall number of the individuals cannot increase on the average. Together with the density-dependent effects (such as hypercompetition), this places a slight limitation on the species production dynamics of the presented model. At the same time, maintaining a meaningfully stable minimal 'base line' ecosystem was considered a key to the study of species emergence.

### Realization details

The model consists of a population of agents and a non-spatial environment shared by them. Each agent has its phenotype represented as a variable length vector of integers from the interval  $[V_{min}, V_{max}]$ . (The length of the vector is always identical for all agents.) The agent's phenotypic traits remain fixed during the lifetime of the agent. In addition to their phenotype, agents only have the minimum of properties: age and accumulated energy.

The evolution engine uses a quasi-parallel activation regime. Each agent gets to act once per every time step in a dynamically randomized order. The agents' activity consists of three steps: energy intake, energy consumption, and reproduction. The agent first seeks  $E_{in}$  units of energy from the shared environment, and, depending on the amount available, it receives  $e_{in}$  units (possibly 0). The efficiency of energy intake decays with age:

$$e_{accumulated} = e_{accumulated} + e_{in} \cdot (E_{discounting})^{age},$$

where  $0 < E_{discounting} < 1$ . Next, the agent consumes  $E_{consumption}$  units of its accumulated energy. If it does not have this amount available, the agent dies. Surviving agents attempt to reproduce with probability  $P_{encounter}$  (i.e. every time step produces part of an entire new generation). Updating the shared environment completes the iteration. This means the addition of  $E_{increase}$  units to the energy pool.

In reproduction an active agent picks a random mate from a list of potential partners, individuals similar enough to bear an offspring with the given agent. Similarity is measured by Euclidean distance between the agents' phenotype vectors. An advantage of this metric is that it is dimension independent. It allows for sexual selection to occur in the same way between any selected phenotype pairs of arbitrary dimensionality. Given two parents, and similarity  $d$  defined as above, the number of

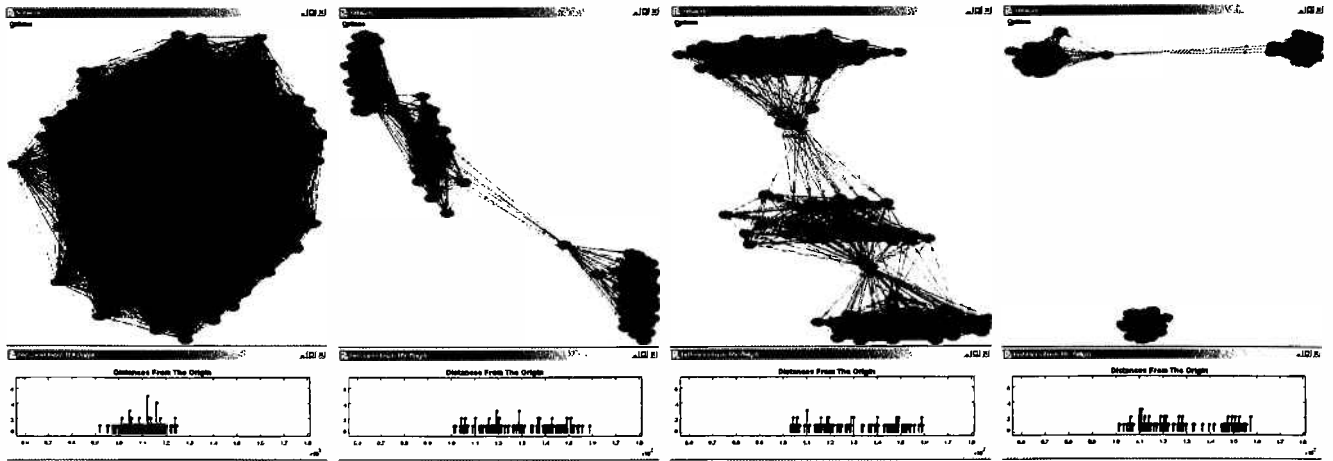


Figure 1. Segregation of a species in a hand-controlled experiment ( $t=75,90,114$ ). Complete separation occurs at  $t=117$ . A stable species splits as a response to the artificial introduction of a new interaction dimension at  $t=75$ . (Old phenotype space was 5 dimensional.)

offspring is  $M_{const} + (M_{limit} - d) \cdot M_{slope}$  (for  $d > M_{limit}$ ). New agents inherit the active parent's phenotype, except for mutation and crossing over that occur with probabilities  $P_{mutation}$  and  $P_{crossing}$ , respectively, per gene. Mutation shifts the value of a gene by a random value in  $[-V_{mutation}, +V_{mutation}]$ . If the mutated value falls outside the interval  $[V_{min}, V_{max}]$ , the offspring is dropped.

A new phenotype dimension is introduced with probability  $P_{change}$  per offspring. When this occurs, a new component is added to the agents' phenotype vector. The particular value an agent receives depends on the used 'stretch' method. The type-based method calculates the value from the agent's old phenotype. For simplicity, only the value  $v$  of a single dimension (the last one) is used:

$$v_{new} = V_{min} + (v \cdot V_{stretch}) \bmod (V_{max} - V_{min} + 1),$$

where  $V_{stretch}$  is a positive parameter. The type-independent method selects a uniform random value from  $[V_{min}, V_{max}]$ .

## Experiments

We conducted several elementary experiments to test how interaction change can affect evolution. All experiments were done on populations with several hundred or a thousand individuals. To minimize complications with hyperspace, in the present, test-of-principles model we kept dimensionality low. In a typical run we started with phenotypes of 5 dimensions. During a run the number has increased to about 50 over a few thousand time steps.

### Hand-Controlled Experiments

We first present a hand-controlled experiment for interaction change (with  $P_{change} = 0$ ). After the population converges to a stable species (Fig.2.left), a new phenotype dimension is added by hand. On the example of a transition from an 5- to a 6-dimensional phenotype, the

Figure demonstrates how the operation changes the distribution of phenotypes without changing the (old) phenotype values. Using the event as 'fuel', the relaxation process of the evolution engine tends to produce one or more new stable species, as detailed on Fig. 1. The networks shown here are results of a Fruchterman – Reingold (1991) algorithm, or spring model (FR). Nodes are organisms, edges show mutual reproduction ability; an absent edge means reproductive isolation between individuals (i.e. connected components are species). Distances in FR are not proportional and the placement is arbitrary. Fig. 1. (bottom part) shows the same time steps represented in one-dimensional true Euclidean distance, measured from the origin of the phenotype space. Height represents the number of individuals at a given distance. We see that a well-defined morphological cluster gets extended because of the introduction of the higher dimension, and it finally splits, in terms of the one-dimensional distance parameter.

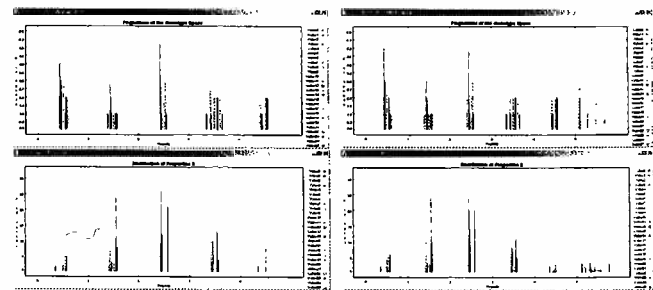


Fig. 2. Distribution of phenotype vectors before (left) and after (right) interaction change in a sample run. Note the role of the new dimension. Both the type-based (top) and type-independent method (bottom) are shown.

In several hand-controlled experiments we invariably found that a species at adaptive stasis (i.e. where there is no other change except drift) destabilizes and tends to

yield offspring species upon the artificial introduction of a new interaction dimension (using either method). Simultaneous FR and phenotype distribution plots (not shown) reveal that the source of this behavior is that different types of new reproduction events occur that rapidly change the species composition and facilitate separation.

### Autonomous Experiments

In a series of autonomous experiments the system was run for 6-12,000 steps (or "generations") with various nonzero values of  $P_{change}$  that introduces new interactions at uneven intervals. Qualitatively, we experienced similar behavior as in the hand-controlled case. With the subsequent change of interaction dimension, a series of speciation event occurs that together with the basic behavior of the evolution engine produces a complicated dynamics of speciation and extinction. Animations from data show that the process is guided by the interaction change events.

Morphological (and functional) separation of emergent species is visualized using a standard ordination method in a sample run in Fig. 3. The phenotype space is 5 and 50 dimensional at the left and the right hand, respectively. Figures come from the same autonomous run.

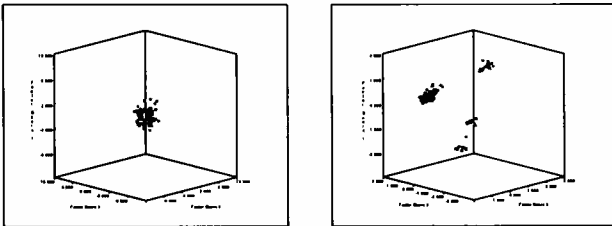


Figure 3. Emergence of species in n-space, shown by correlation-based 3-factor analysis (using SPSS). Scale is arbitrary & varies.

Theoretically, it is possible that several factors other than interaction change (such as the growing mutational load in higher dimensions) are also responsible for the experienced behavior in autonomous runs. However, hand-controlled experiments and convergence of the basic engine indicate that the former is a sufficient condition.

Discussion will be left to sensitivity analysis (below).

### Artificial Phenotypes and Interaction Change

Our primary motivation is to demonstrate the evolutionary effects of interaction change in abstract form. Yet there is a temptation to seek biological meaning in our procedures. A complete discussion of the issue is left to another paper.

The type-based method assumes a simultaneous switch in the entire population at the time step when a new interaction for a single organism is introduced. This is unrealistic but less artificial than it seems. Phenocopies, bistability of selected traits, and environmentally induced epigenetic effects can equally produce similar transitions. The chosen method, at the same time, conserves the

number of different phenotypes during interaction change. This limits arbitrariness in the model by constraining the newly introduced variability in the population.

The type-independent method spreads the species in hyperspace, giving more chance for distant regions to be occupied by organisms that may find new sexual matches among themselves. Biologically, this corresponds to the case where despite the homogenization of overt traits due to selection, a significant hidden variability remains there in the unused phenotype traits, to become expressed later.

As clarified by the analysis below, the behavior of the model was insensitive to the choice between the two assignment methods. In future models, an obvious task would be to study the effect of different biologically meaningful assignments, down to single point mutations. A further objective is to allow emergent species to drop some of the old interaction dimensions, further structuring global interaction space. Finally, allowing more complex phenotype-based interactions (such as predation) would yield ecosystems with emergent producers and consumers that avoid sharing the same resources as here.

### Sensitivity Analysis

To test the robustness of our results, we conducted extensive experiments with various parameters. We varied each parameter in a wide range, while keeping the rest at its default value. These studies yield results consistent with the experiments above. The more detailed analysis, and discussion of the mechanisms of species evolution (to rule out trivial effects) are left to a Technical Report (Gulyas 2004) and to a subsequent paper, respectively.

$V_{min}$	0	$M_{limit}$	15
$V_{max}$	100	$M_{slope}$	0
$P_{encounter}$	0.1	$M_{const}$	1
$P_{crossing}$	0.2	$E_{consumption}$	5
$P_{mutation}$	0.1	$E_{in}$	10
$V_{mutation}$	2	$E_{discounting}$	0.9
		$E_{increase}$	1000

Table 1: Default parameter settings.

### Experiments with the Evolution Engine

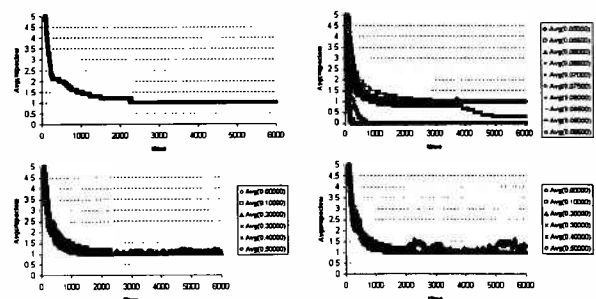


Figure 4. From top-left: basic behavior; effects of varying  $P_{encounter}$  (in the range 0.05-0.095),  $P_{mutation}$ , and  $P_{crossing}$  (10 different random seeds; 6,000 steps)

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For these experiments we initially placed agents in a hypersphere of diameter 30 using a uniform random distribution. Under the parameter settings studied, sexual selection plus hypercompetition led to a fast convergence to one species from the about 25-30 in the hypersphere (see Gulyas 2003 and Fig.4.). The value of  $P_{encounter}$  was tested in the interval [0.05, 0.095]. The evolution engine produces its basic behavior for  $P_{encounter}$  values above 0.065. At lower probabilities the population gradually becomes extinct due a to lack of sufficient reproduction. To speed up the processes of interest, we introduced high probabilities for mutation and crossing over. Both were tested in the range 0.1-0.5. As demonstrated in Fig.4., basic convergence to one species is robust against these values. (The system trivially converges when any of the two parameters is set to 0.) The behavior of the evolution engine is robust across a wide range of  $V_{mutation}$  values (i.e., 1-10) as well. The number of species drops down to a few ( $\geq 1$ ) and stays there. Higher values yield more species, but the number of constant species is relatively low even for extreme values of the mutation parameter.

Similarity-related parameters were also tested:  $M_{limit}$  in the interval [0, 20],  $M_{slope}$  between 0 and 2.0, and  $M_{const}$  in the range of 0-10. Of these parameters, only the first has a pronounced effect. For  $M_{limit} \geq 5$ , the engine converges to a single species, while lower values increase the number of constant species, as the possibility of mating will be fairly low among agents with different phenotypes. At  $M_{limit} = 0$  the population dies off.

Naturally, the system is more sensitive to the energy-related parameters. If  $E_{consumption}$  (tested in the interval [1, 10]) is above 6 (with  $E_{in} = 10$ ), the population goes extinct. Otherwise, the dynamics settles down to a single species. Similarly,  $E_{in} > 9$  yields a single species, while other values (tested in the range 5-25) kill off the population. The empirical limit for  $E_{discounting}$  is 0.875. For values below that, agents get old too soon to survive. For other values in [0.8, 0.975], the engine produces a single species. (The speed of convergence is roughly inversely related to the value of the tested parameter.)

With  $E_{in}=10$ , an agent population of size  $\geq 100$  needs at least 1000 units of energy input per time step.  $E_{increase}$  was tested in the interval [900, 2000]. This produces a single species. Higher values yield longer-lived agents, and slow down convergence.

## The Evolution of Species

In the evolution engine we experience fast convergence to a single species. However, as shown on Fig.5., the gradual introduction of new phenotype dimensions at  $P_{change} \neq 0$  results in a growing number of reproductively isolated groups, i.e. species. As the energy-system can only support a certain number of individuals, there is a natural upper limit to this. Apart from this, interaction change as simulated in this model yields a persistent evolution of new species.

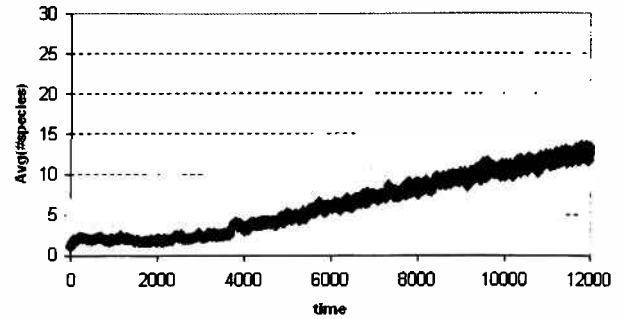


Figure 5. The evolution of species. Graphs show the average number of species (connected components of FR networks) versus time, using default settings (in 10 runs). Error bars show minimum and maximum numbers.

$P_{change}$	0.0075
'Stretch' method	Type-based/ Type-independent
$V_{stretch}$ ( type-based only)	2

Table 2: Default values for the interaction change parameters.

There are three parameters related to interaction change, as summarized in Table 2. In a limited test, we experimented with changes imposed on these, one by one. Changing  $P_{change}$  between 0.0005 and 0.001 yields results similar to those shown already. The number of species undergoes a monotonic growth. The curve gets steeper for higher values of the parameter, with the number of produced species falling between 5-15 after 12,000 iteration, and increasing with the parameter value.

The value of  $V_{stretch}$  was varied between 1 and 20. As shown on Fig.5., the results are similar to the default behavior, although higher parameter values yield higher variance. Finally, the type-independent 'stretch' method also reproduces the qualitative hand-controlled results, although again with a much greater variance (Fig.6.).

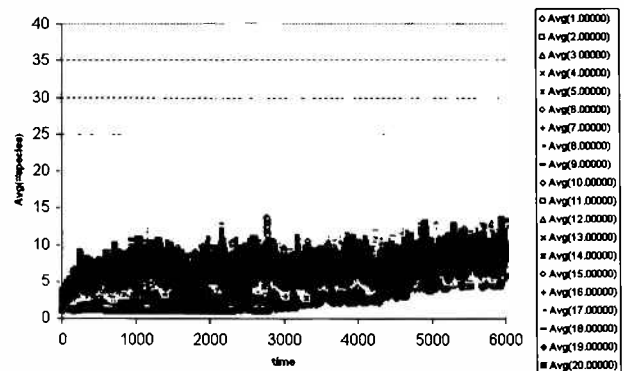


Figure 5. Effect of different values of  $V_{stretch}$ . Graphs show the average number of species versus time (10 runs), with default settings. Error bars show minimum and maximum values.

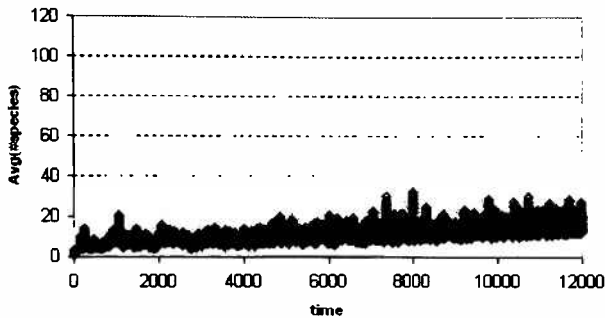


Figure 6. Evolution of species with a type-independent method. The average number of species (10 runs) versus time using default settings. Error bars show minimum and maximum values.

## Conclusions

In this paper we presented a first simulation report of an interactions-based evolutionary model (kept in development for more than a year). The model uses similarity-based sexual selection to approach open ended evolution. We demonstrated that changing phenotype-to-phenotype interaction (adding new dimensions to interaction space) can repeatedly split species by the production of new selection constraints. We hypothesize that sustained ecological evolution proceeds by similar mechanisms. Prospects for further studies have been briefly outlined.

The current version of the simulation is downloadable from the site <http://hps.elte.hu/~gk/EvoTech/>.

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