

On the Degree of Freedom in Multilevel Evolutionary Models

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Biotic systems have a high degree of freedom subject to evolution, but also have constraints and semi-invariant structure (e.g. RNA/protein folding is not random). A common approach to model biological evolution is to construct a “biologically” pre-structured system with a few mutable parameters—i.e. a small degree of freedom—and to study the strengthening/weakening of the predefined structure (example below). Although we consider it essential for better understanding, this approach does not allow us to study the emergence of novel structures. To go beyond this, we recently investigated a multilevel evolutionary model that incorporated both a high degree of freedom and biologically relevant structure (Takeuchi and Hogeweg 2008). We first review this study and then compare it with another study where we investigated an evolutionary model with a considerably smaller degree of freedom (Takeuchi and Hogeweg 2009); therewith we present some interesting insight on the the degree of freedom in evolutionary models.

We investigated the evolution of RNA-like replicator systems by explicitly modeling the genotype-phenotype-interaction mapping of individuals (Takeuchi and Hogeweg 2008). By using RNA folding and base-pair-matching based molecular recognition, we incorporated complex structure and a high degree of freedom into the genotype-phenotype-interaction mapping. The results showed that a population, originally consisting of one genotype, evolved into a complex ecosystem consisting of up to four quasi-species through a chain reaction of niche generation and speciation, where a replicase species generated a niche for a parasite species, of which evolution generated a niche for an “escaping” replicase species and so on. Through this diversification, evolution generated unique classes of genotypes and phenotypes having distinct ecological functionality, which was not “built-in” to the model.

That said, let us now consider more of a behind-the-scenes story. Initially, we were confronted with the results of the simulations, which were just millions of genotypes present in the system over time, an apparently unintelligible mess of data. Among numerous means to analyze the data, bioinformatic pattern detection devices (viz. phylogenetic trees and sequence-logo) turned out to be the most useful in this case. These devices enabled us to realize the existence of sequence classes and associated sequence patterns; stated differently, we discovered “meaningful observables” of the system. We re-ran simulations with each individual being identified by observables “designed” to distinguish the recognized sequence classes. The results revealed a sequence of “events described in

terms of the right observables”. Then, it was a simple matter to understand the dynamics of the model as a process of evolutionary adaptations as explained above. This very simplicity implies the importance of the general results such as the ecological organization evolving in the system. However, it by no means implies that they are foreseeable, let alone the specific patterns evolved in the sequence, secondary structure and spatio-temporal distribution of individuals.

For comparison, we next review another modeling study of replicator evolution with a considerably smaller degree of freedom (Takeuchi and Hogeweg 2009). In this model, we predefined two classes of replicators: replicase and parasite. Each parasite was characterized by two parameters. One specified how often a parasite rendered itself accessible to replicase—unfolding parameter u . The other specified how well it was recognized by replicases if accessible—recognition parameter r . We investigated the evolution of these two parameters. In a well-mixed system, parasites evolved greater u and r , which obviously increased their “fitness”; consequently, the whole system collapsed due to over-exploitation. However, if replicators were compartmentalized by vesicle-like boundaries (i.e. protocells), the system survived because of multilevel selection. Since too strong parasitism—i.e. too great u or r —was disadvantageous at the protocell level, the system displayed a trade-off curve $f(u, r) = 0$. Interestingly, along this curve, novel long-term evolutionary trends emerged. If the mutation rate of parasites was high, long-term evolution increased u and decreased r . Conversely, if the mutation rate is low, it decreased u and increased r . These trends were explained as a process of evolutionary adaptations: If the mutation rate is high, the evolution of stronger parasites is fast, so that the replicator system within a vesicle is likely to be deterministically unstable; in this case, weakening the deterministic flow of the internal replicator dynamics is adaptive because it effectively relaxes the parasitism. It turned out that this caused the increase of u and the decrease of r (the reversed argument holds for lower mutation rates). Here, in contrast to the previous study, we a priori knew the meaningful observables (i.e. u and r). We thus recognized the emergence of novel evolutionary trend trivially. However, to explain this as adaptation required us to analyze the model’s dynamics at multiple levels and to consider the interactions between them, which was hardly trivial, let alone the explanation we obtained.

Comparing these studies, we conceived the following notion. The evolutionary process can be seen as a “sensitive” and “inventive” generator—and therefore detector—of adaptations. In multilevel evolutionary models, it is nearly impossible to foresee what adaptations evolution generates whether the degree of freedom is small or large. However, depending on the available degree of freedom, evolution seems to generate different kinds of adaptations. If the degree of freedom is small (i.e., the restriction is strong), evolution sensitively detects adaptive features and generates them, which, to us, are easily recognizable, but intricate—or subtle—in their adaptive effect. If the degree of freedom is large, evolution detects possible adaptations and inventively generates the best (also with respect to attainability and maintainability), which, to us, are non-trivial to recognize due to the lack of search images and predefined observables, but

are, in hindsight, obviously adaptive and hence important (here, subtle adaptations might be like stars in daylight). This notion prompts us to study evolution with a complex genotype-phenotype-interaction mapping with a high degree of freedom (cf. Hogeweg 1998).

References

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