

# Complexity in Speciation: Effects of disasters on adaptive radiation in a Dual Phase Evolution model

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Changes in landscape structure can greatly affect biological evolution, but the role of such changes in generating macroscopic patterns is still poorly understood [1]. Recent studies suggest that principal processes in species evolution in landscapes are an instance of a mechanism observed in a wide range of complex systems, which we have termed Dual Phase Evolution (DPE) ([2], [3], [6]). Here, we investigate whether mass extinctions induce DPE in a simulation model of adaptive radiation.

According to the DPE hypothesis, evolution in landscapes exhibits two phases – selection and variation. Adaptive radiation is typically rare during a selection phase and common during a variation phase [3]. Disturbances such as mass extinctions can flip the landscape from selection to variation phases. In biological evolution, this hypothesis may help to explain the observed pattern of punctuated equilibrium, where long periods with little evolutionary innovation are interrupted by periods of rapid adaptive radiation [5]. Similar processes have been shown to occur in a wide range of complex systems, including artificial, biological and social ([2], [6], [3]).

We simulated a large population of agents situated on a two-dimensional homogeneous landscape. The model is based on a well-known model of adaptive radiation which did not incorporate DPE [4]. The landscape consists of a 100x100 grid of cells. Each cell can accommodate up to 5 agents. The landscape contains 1 global and 100 special niches, where each niche is represented by a string of 15 bits. Each agent must adapt to the global and one of the special niches by evolving a genotype that represents 2 strings of 15 bits. The fitness of an agent is determined in proportion to the linear combination of the hamming distances between the agent's genotype and the respective niches. The agent's special niche is always chosen on the basis of its current genotype as to maximise the fitness. Reproduction involves free recombination and mutation with a small probability, therefore an offspring of two agents adapted to two different special niches is likely to be poorly adapted to either niche. In this respect, sub-populations adapted to different species are reproductively isolated and can be said to represent different species [8].

We initialised the landscape with a small population of clones of two randomly chosen individuals and thereafter simulated the model for 40000 non-overlapping generations. Our observations are in-line with the findings reported in [4]: after an initial burst of adaptive radiation during the first few thousand generations the system typically enters a selection phase that lasts for the remainder of the experiment. There, the proportions of the total population taken up by particular species remain approximately constant or change very slowly in accordance to the species' average fitness.

In a series of experiments we simulated a mass extinction by killing all agents at 95% of the cells. A mass extinction occurred with a small probability (0.0001) at each generation. Over long periods, mass extinctions enhanced diversity within the model. At many occasions, after the model landscape was fully re-populated following a disaster, a significant proportion of the total population was taken up by species which did not play a significant role in the model ecology prior to the disaster.

In a further series of experiments we varied the method by which the cells affected by a mass extinction were selected. Initially we selected 95% of cells uniformly randomly distributed across the landscape. Such extinctions had only a small effect on the species composition of the

population, which suggests that the degree of landscape connectivity is not the only factor affecting phase changes in species evolution in landscapes. Next, we used a selection method in which the model landscape was bombarded with extinction impacts which wiped out all cells within a certain radius around a randomly selected centre. This continued until 95% of cells were wiped out. As the result of this, the remaining population was distributed on several islands with large empty areas in-between. Mass extinctions caused by this method were followed by phases of evolutionary variation at many occasions.

While the precise relationships between the spatial configuration of the disasters and their evolutionary effects remain to be investigated in future work, we can conclude that the size of the disaster impacts plays an important role in these relationships. We suggest that vast empty areas located between the remaining population-islands favour variation phases because they present spaces into which the remaining populations can expand without having to compete with existing occupants. Large disaster impacts are also more likely to skew the statistical properties of species distributions. In the context of low landscape connectivity this leads to a situation where global and local competition are low, which favours adaptive radiation and the long-term establishment of newcomer species.

In summary, our results confirm that mass extinctions caused by external disturbances are capable of flipping the evolutionary process from a selection phase into a variation phase therefore punctuating phases of little evolutionary innovation with phases of rapid species turnover and adaptive radiation.

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**Short abstract:**

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Recent studies suggest that macro-evolutionary patterns such as punctuated equilibrium [5] may be generated by a process termed Dual Phase Evolution (DPE) ([1], [2], [3]). According to the DPE hypothesis, evolution in landscapes exhibits two phases – selection and variation. Disturbances such as mass extinctions can flip the landscape from selection to variation phases. Similar processes occur in a wide range of artificial, natural and social complex systems ([2], [3], [6]). Here, we show that mass extinctions induce DPE in a simulation model of adaptive radiation. The model is based on a previous model of adaptive radiation which did not incorporate dual phase evolution [4]. Results confirm that mass extinctions caused by external disturbances can trigger periods of rapid species turnover and adaptive radiation (variation phases), which are followed by long periods without innovation (selection phases). Our simulations also show that the spatial configuration of disasters leading to mass extinctions strongly influences whether and to what extent such disasters are capable of inducing evolutionary variation phases.