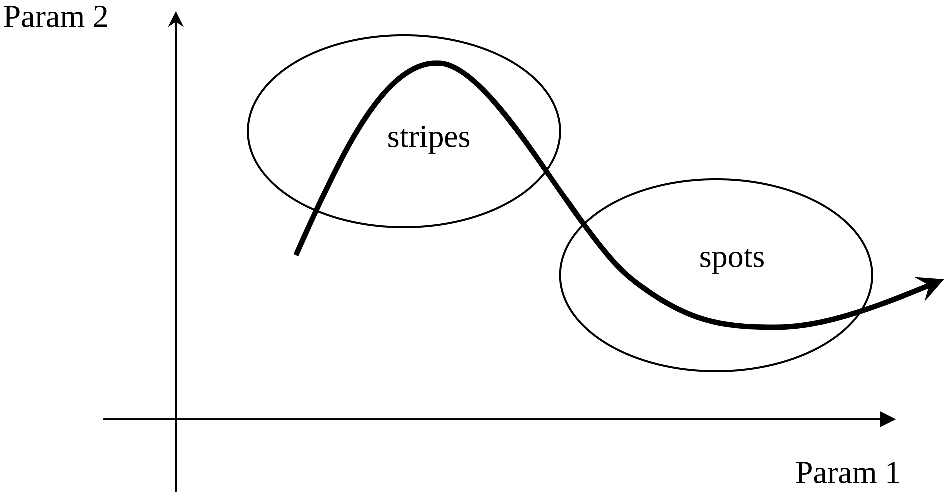
# Evolutionary Pattern Formation

NB. Additions in italics

The problem of explaining the rich spectrum of different patterns exhibited by mammals has a long history. In a controversial paper (1952) Turing proposed a Reaction-Diffusion (RD) model to explain at a macroscopic scale the process of pattern formation, as related to the occurrence of what he called a diffusion-driven instability. A typical Turing system consists of at least two chemical species, usually referred to as activator and inhibitor, reacting in such a way that their steady state is stable to small perturbations in the absence of diffusion, but becomes unstable when diffusion is present. This simple mechanism (also referred to as Turing instability) was indicated by Turing as being responsible for the creation of spatial patterns in mammals.

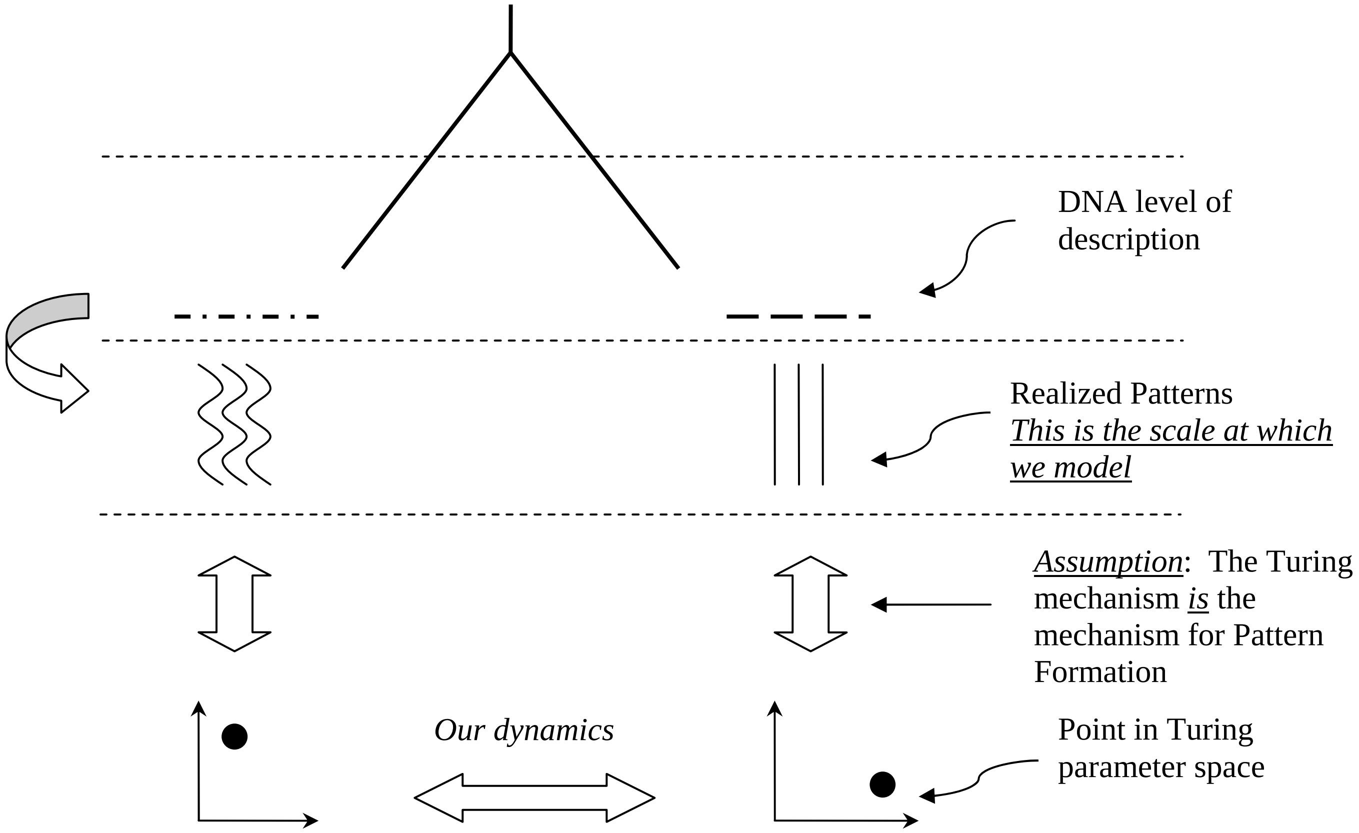
Later on Oster and Alberch (1982) reconsidered the pattern formation process in mammals from an evolutionary perspective. They associated mutations at the genetic DNA scale with the morphologies realized at the phenotypic scale. In particular, the structure of the phase space (the so-called bifurcation diagram) for Turing-like systems accounts for the possibility that random fluctuations at the DNA scale either can be filtered out, and give qualitatively stable phenotypes, or can accumulate, inducing thereby speciation events.

We propose to take up this issue again, and develop a stochastic *evolutionary model of the evolution of a* Turing model that accounts for evolutionary randomness directly at the phenotypic scale. *This model only applies to the phenotypic level and makes no statement about the underlying genetic mechanism. From a mathematical point of view this will correspond to inserting noise in deterministic Turing models in order to reproduce variation of patterns within the same domain, as well as transitions among different domains (for instance from spots to stripes).The simplest way to do this is to let the Turing parameters {a} evolve in time by simple Brownian Motion, and let them explore the parameter space. I.e., if a is one such parameter, we shall assume* $a = a(t) = a_0 + x(t)$, *where x(t) is a random variable, normally distributed, with zero mean and delta correlated.*



*In the Figure above we have, for simplicity, plotted a two-dimensional representation of a multidimensional parameter space (one dimension for any parameter) with the ovals identifying the regions of parameters in which different patterns are produced. The thick arrow corresponds to the exploration of such a parameter space induced by the dynamics introduced on the Turing parameters. It is obtained by measuring the system at given intervals of time. Noisy fluctuations are not represented in the picture.*

*In the next Figure, we show the interpretation of such a model from an evolutionary perspective. A simple phylogenetic tree is shown, and its leaves can be labeled at different scales. The 'microscopic' scale is at the level of genes ('DNA level of description'), while the macroscopic scale is at the level of patterns. Once again, we are not concerned with the modeling of sequence evolution, but rather focus on the modeling of phenotypic diversity at the level of patterns, where we make the assumption that patterns are produced by means of a Turing mechanism. In the same picture, the parameter space is schematized again, to show how to associate a specific pattern to a point in the parameter space. The stochastic dynamics defined on the Turing parameters should allow you to 'run' along the branches of the phylogenetic tree.*



Once the model is defined in the way mentioned above, we shall proceed to a careful study of its properties, using both analytical and numerical methods. A final step of the project will involve parameter estimation, and comparison with phylogenetic data. *In principle, it should be possible to construct a maximum likelihood phylogeny from a series of observed patterns using such a model.*

*As a final remark we would like to mention that besides Brownian Motion, we plan to explore other possible dynamics of parameters such as correlated noises or specific driving forces. Also, we would like to study the relationship between sets of Turing parameters and realized patterns, and discuss the uniqueness of their correspondence.*

A brief description of the work involved is as follows. The starting point will be at a basic level, developing further into more complex issues.

- Deterministic Model
  - Studying basic literature and familiarizing with RD Turing systems.
  - Choose a specific RD system exhibiting Turing instability
  - Analysis
    - Perform linear stability analysis
    - Bifurcation diagrams

  - Numerics
    - Simulate the system (Matlab, or other programming language)
    - Obtaining different patterns and studying the phase space
    - Compare with analytical predictions

- Definition of the Stochastic Model

  - Studying basic literature on noise in spatially extended systems. In particular:
    - Additive noise
    - Multiplicative noise
  - Understanding how to define an evolutionary Turing-like model with noise. Explore:
    - Additive noise
    - Multiplicative noise
    - Other types of noise?

- Study of the Stochastic Model

  - Analysis as in the deterministic model (if possible)
  - Simulations as in the deterministic model

- Mapping of the model to real phylogenies

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