Was Wright Right? Reconsidering the Adaptive Landscape

Maxwell Shinn and Clarence Lehman

Department of Ecology, Evolution, and Behavior, University of Minnesota

University of Minnesota
Supercomputing Institute

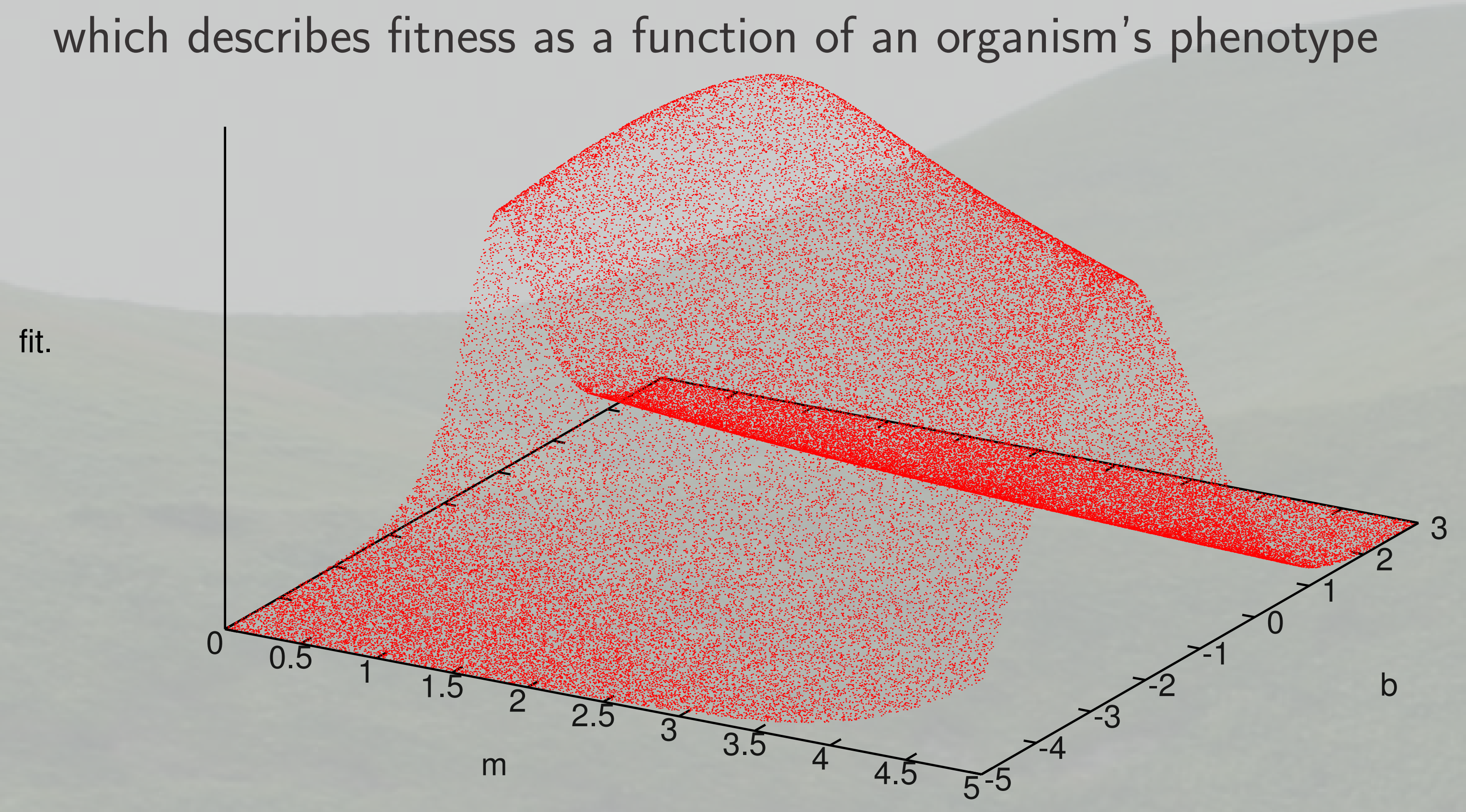
Introduction

The adaptive landscape, first proposed by Sewall Wright (1932), is a high-dimensional surface that defines how populations evolve. There are three types of landscapes:

Genotypic fitness landscape The original conception of Wright, where relative evolutionary fitness is plotted as a function of an organism's genotype

Genotypic ratio landscape The interpretation of Wright's work by statistician Ronald Fisher, where fitness is plotted as a function of a population's genotypic ratios

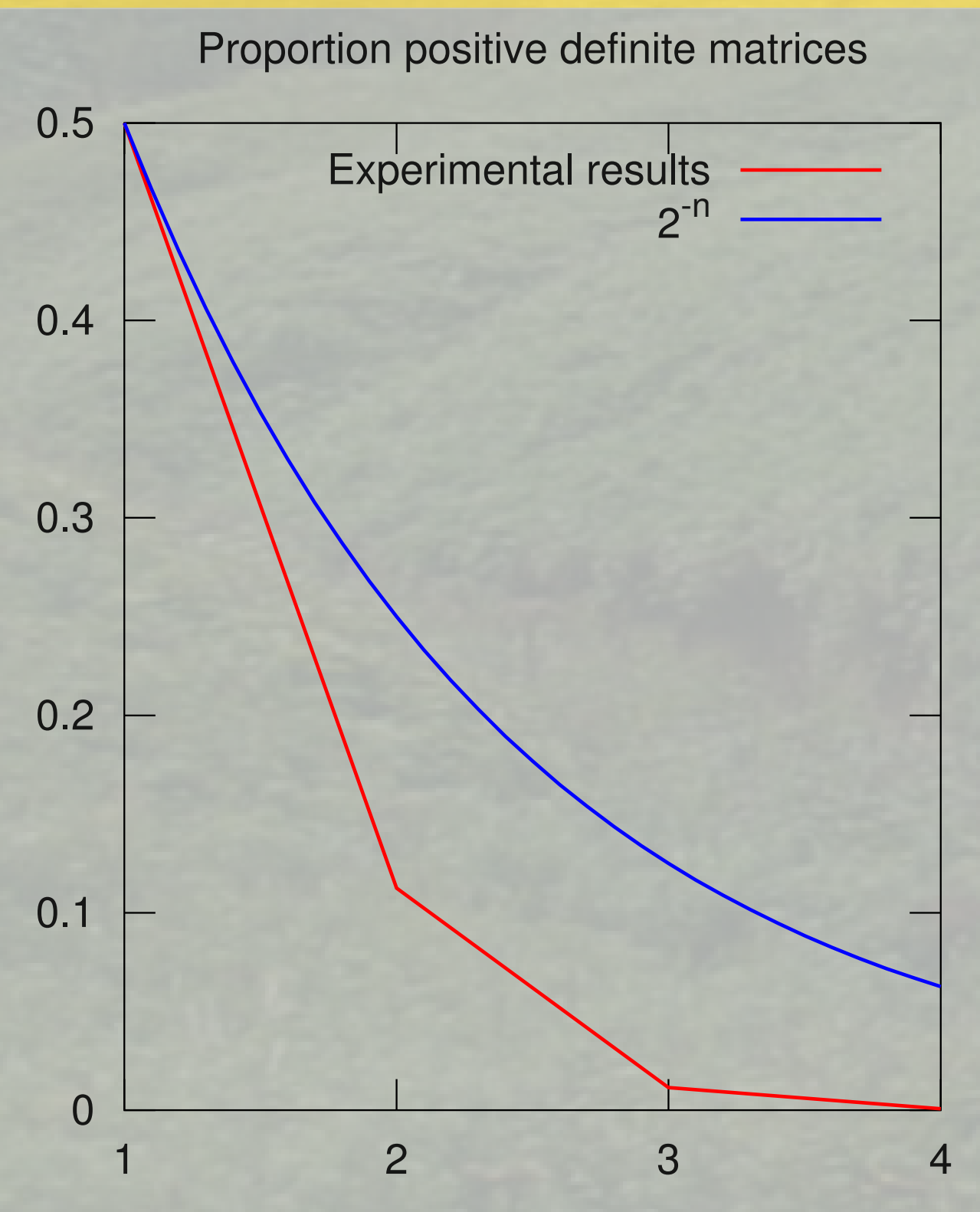
Phenotypic adaptive landscape A landscape envisioned by G. G. Simpson, which describes fitness as a function of an organism's phenotype



Wright hypothesized that populations would evolve until they reach a peak on this landscape, as on the landscape above.

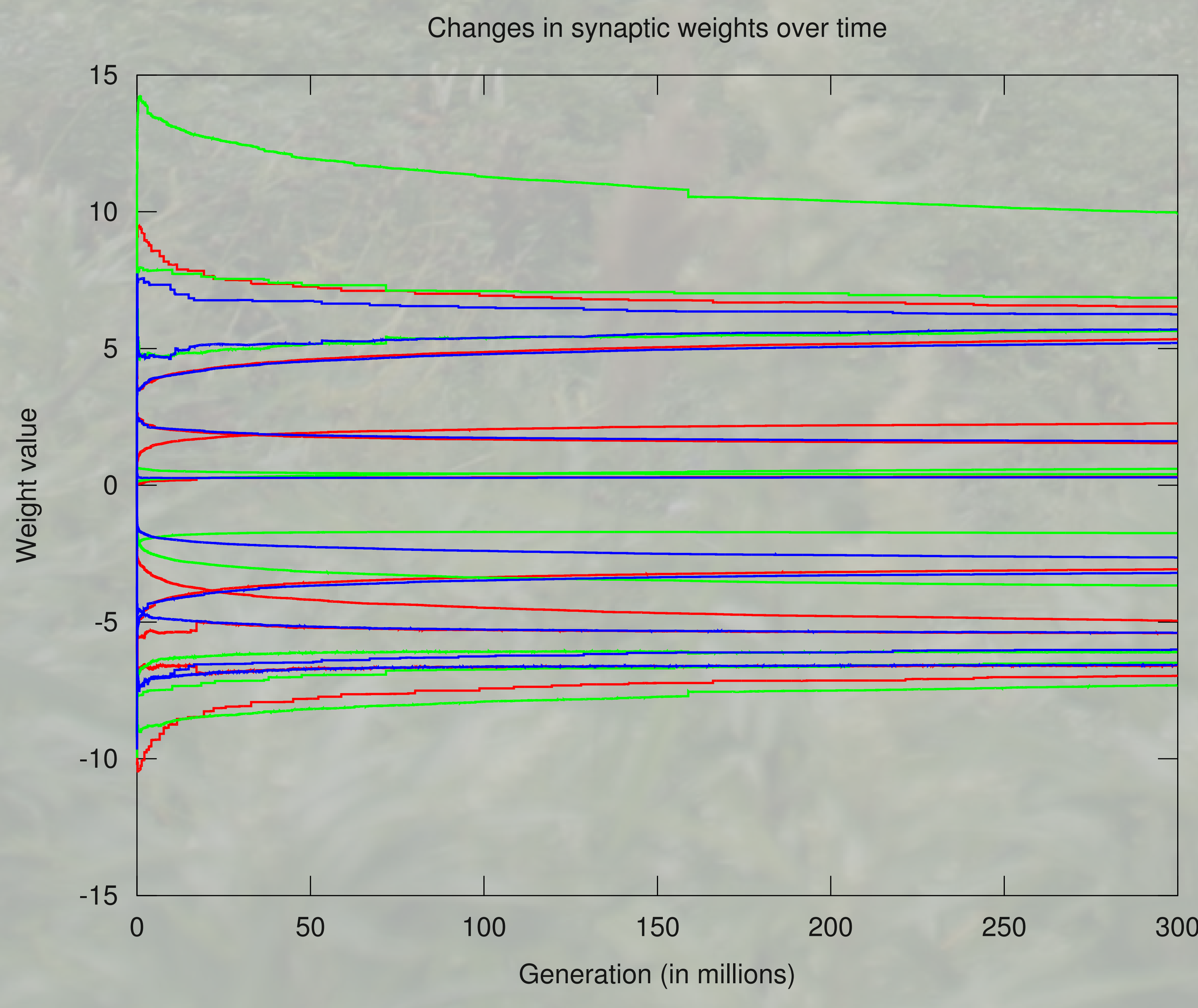
Peaks of random surfaces

Fisher rebutted Wright, suggesting that there would be very few peaks on high dimensional landscapes. If all partial derivatives are zero at a point, it is possible to determine whether this is a maximum or not by looking at the eigenvalues of the Hessian matrix. We approximated this by generating random matrices from a Gaussian distribution and found the following distribution.

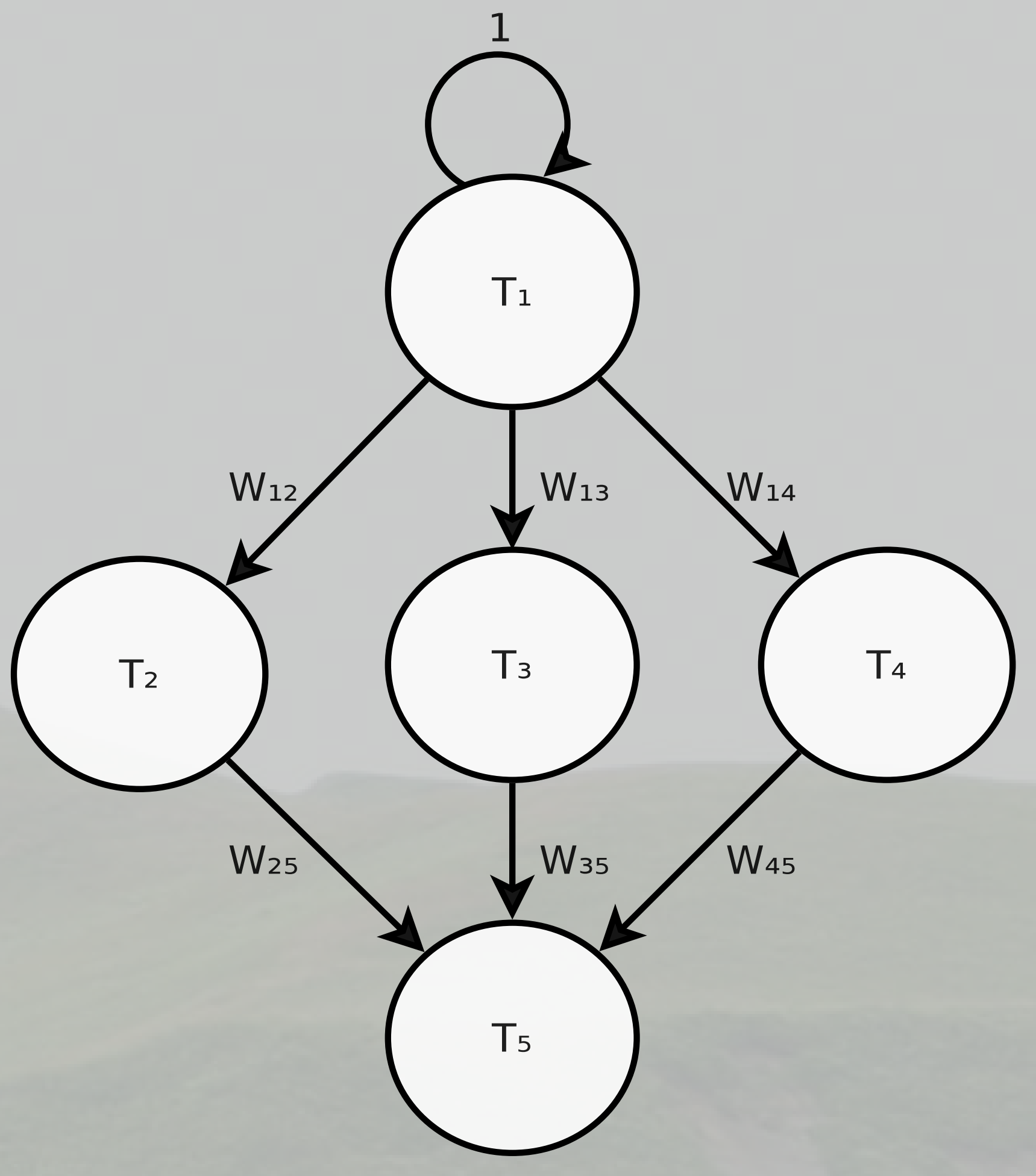


Macroscale

In low-dimension simulations on the macroscale, it appears Wright was right. In a ten-dimension simulation, the weights of each simulation (plotted in different colors) appear to converge to different values, suggesting the presence of multiple peaks. Similar behaviors were observed in our largest simulation of 25 dimensions.



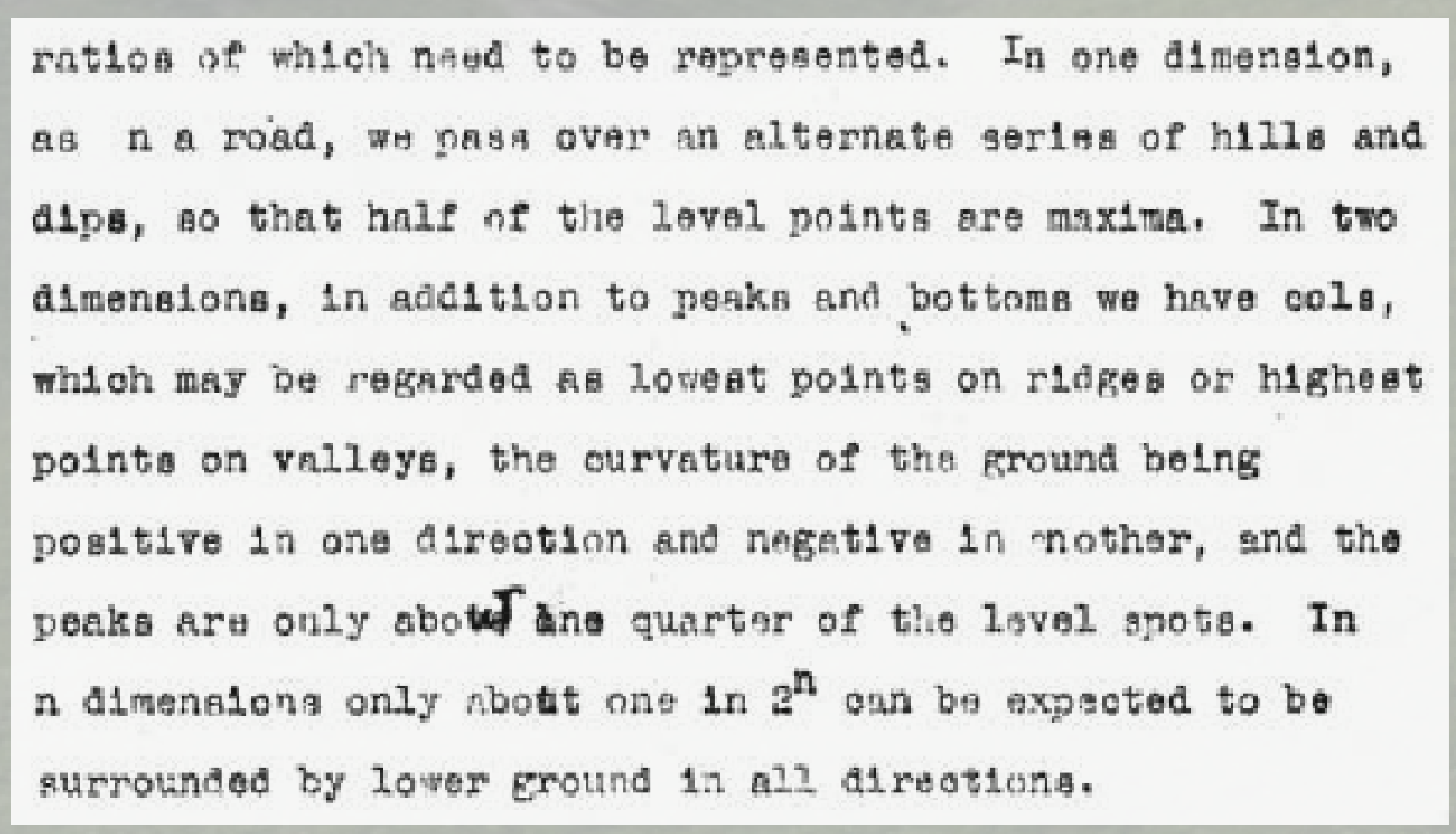
Artificial Neural Networks



- Artificial neural networks (ANNs) are high-level models that can perform computations in a biologically-relevant manner
- ANNs can be trained using an algorithm that mimics natural selection
- All possible "genotypic combinations" (connection weights) create a genotypic fitness landscape
- Where $\mathbf{S(x)}$ is a sigmoid function, $\mathbf{W}$ is the connection strength matrix, $\vec{\mathbf{T}}$ contains thresholds and $\vec{\mathbf{R}}_\mathbf{t}$ contains firing rates at time $\mathbf{t}$,

$$\vec{R}_{t+1} = S(W^T \vec{R}_t + \vec{T})$$

Fisher's views of Wright's fitness landscape



ratios of which need to be represented. In one dimension, as n a road, we pass over an alternate series of hills and dips, so that half of the level points are maxima. In two dimensions, in addition to peaks and bottoms we have cols, which may be regarded as lowest points on ridges or highest points on valleys, the curvature of the ground being positive in one direction and negative in another, and the peaks are only about one quarter of the level spots. In n dimensions only about one in 2^n can be expected to be surrounded by lower ground in all directions.

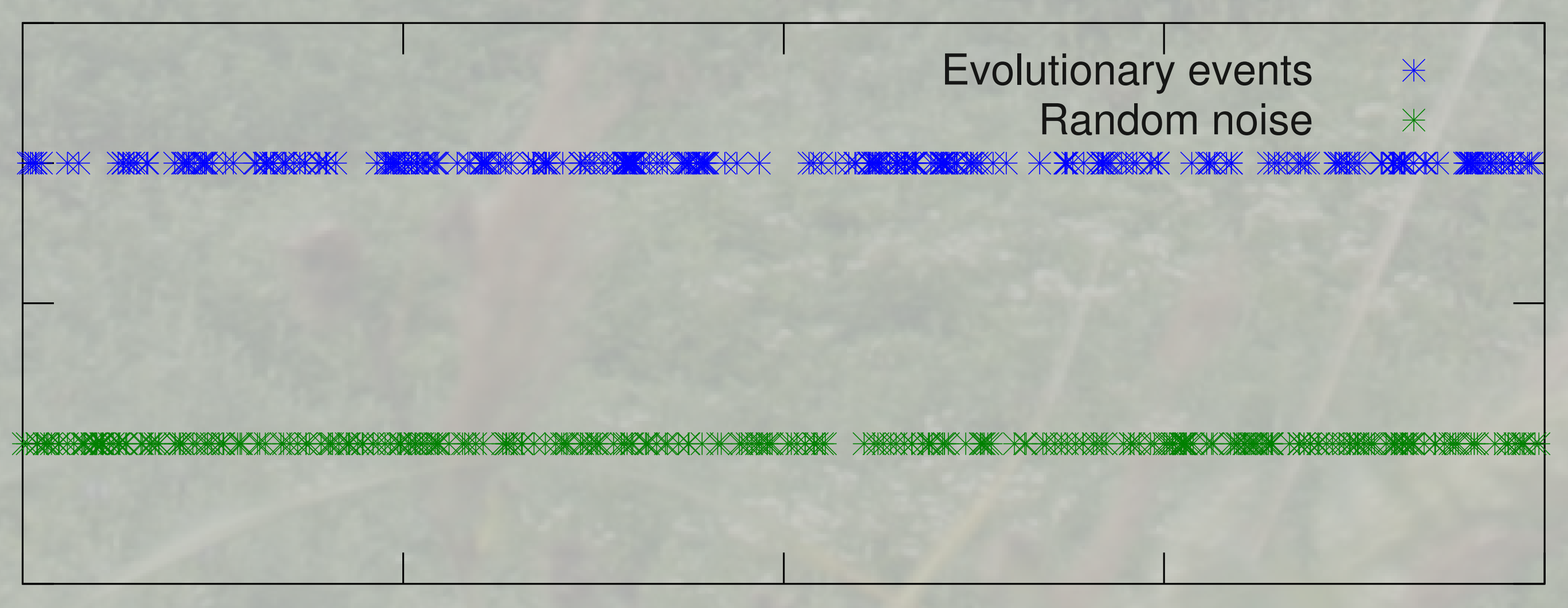
—Excerpt from a letter from Fisher to Ford, May 2, 1938

Directions in n-dimensions

In one dimension, there are two cardinal directions: right and left. In two dimensions, there are 4 cardinal directions and 4 intermediate directions for a total of eight: N, S, E, W, and NE, SE, NW, SW. In $\mathbf{n}$ dimensions, there are $\mathbf{2n}$ cardinal directions and $\mathbf{3^n - 1}$ total directions. Thus, in order to fully "explore" genotype space at a point, it would take at least $\mathbf{3^n - 1}$ organisms.

Microscale

On a small scale, there is evidence of short spurts of rapid evolution followed by stationary periods.



This was confirmed by comparing the distribution of interspike interval to the Poisson distribution.

Future direction

- Look at higher-dimensional landscapes for similar behaviors
- Display structural characteristics of the landscape as evolution proceeds
- Use more complex and biologically-relevant training functions
- See how these patterns change on a genotypic or quantized landscape