

## Evolution of robustness

Wagner [1996] and Siegal and Bergman [2002] have studied a simple model of the evolution of a network of  $N$  genes, in order to explain the observed phenomenon that systems evolve to be robust. In the Wagner [1996] model the gene interactions are represented by an  $N \times N$  matrix  $W$ , whose elements  $w_{ij}$  indicate the effect on gene  $i$  of the product of gene  $j$ , which may involve activation ( $w_{ij} > 0$ ) or repression ( $w_{ij} < 0$ ). Changing expression levels are modeled by the set of difference equations:

$$S_i(t+1) = \sigma \left[ \sum_{j=1}^N w_{ij} S_j(t) \right] \quad (1)$$

where  $\sigma$  is the sign function;  $\sigma(x) = 1$  if  $x > 0$ ,  $\sigma(x) = -1$  if  $x < 0$ , and  $\sigma(0) = 0$ .  $h_i(t) = \sum_{j=1}^N w_{ij} S_j(t)$  represents the sum of all regulatory effects of all of the network genes on gene  $i$ . Ignoring the possibility that the sum is exactly zero, which in our model will have probability 0,  $S_i(t)$  only takes the values  $-1$  (not expressed) or  $1$  (expressed).

These authors primarily considered the case  $N = 10$  and used simulations to reach their conclusions that evolution leads to a population of networks that are more robust to perturbation compared with the founding population. We investigated this model in more detail, considering systems of different sizes with and without recombination, and with selection for developmental stability instead of selection for a specified genotype. Developmental stability in this context means that the dynamical system describing the switching on and off of genes converges to a fixed state of expression levels. Our results show that, given a sufficiently large population size, the qualitative observation that systems evolve to be robust, is itself robust, as it does not depend on the details of the model. In simple terms, robust systems have more viable offspring, so the evolution of robustness is merely selection for increased fecundity, an observation that is well known in the theory of neutral networks. (see Huerta-Sanchez and Durrett [2007]).

## References

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