

topologies. In this work, we study the effect of a modular topology in RBNs. We find that modularity changes the properties of RBNs. Given the fact that real GRNs are modular [38, 8, 37] and most RBN studies have been made over random topologies, it is important to understand the differences between random and modular topologies.

Modularity plays an important role in evolution [42, 14, 50], since separable functional systems are found at all scales of biological systems [48]. Modularity allows for changes to occur within modules without propagating to other regions and the combination of modules to explore new functions [13]. Thus, the study of modular RBNs is also relevant for understanding the evolution of GRNs.

In the next section, classic RBNs are reviewed, together with their dynamical properties and related work. Section 3 presents our model of modular RBNs. Methods and results of statistical experiments follow in Section 4. The discussion in Section 5 reflects on the results and provides an analytical confirmation. Several future research avenues are mentioned to conclude the paper.

## 2 Random Boolean Networks

Random Boolean Networks (RBNs) [25, 26, 16] consist of  $N$  nodes with a Boolean state, representing whether a gene is active (“on” or “one”) or inactive (“off” or “zero”). These states are determined by the states of  $K$  nodes which can be considered as inputs or links towards a node. Because of this, RBNs are also known as NK networks or Kauffman models [3]. The states of nodes are decided by lookup tables that specify for every  $2^K$  possible combination of input states the future state of the node. RBNs are random in the sense that the connectivity (which nodes are inputs of which, see Figure 1) and functionality (lookup tables of each node, see Table 1) are chosen randomly when a network is generated, although these remain fixed as the network is updated each time step. RBNs are discrete dynamical networks (DDNs), since they have discrete values, number of states, and time [53]. They can also be seen as a generalization of Boolean cellular automata [52, 15], where each node has a different neighborhood and rule.

RBNs have  $2^N$  possible network states, i.e. all possible combinations of Boolean node states.