How do complex and robust phenotypes evolve?

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The morphology of multicellular organisms is built by the interactions between genes, cells and environment in a process called development. This study aimed to determine how organisms can evolve complex and stable morphologies. We define complexity as the amount of morphological information in the embryo and developmental stability as the ability to produce the same morphology from the same genetic, epigenetic and environmental conditions in spite of molecular and cell-level noise. To address this question, we explored the space of possible developmental networks by randomly building a large number of them. We then simulated these networks with EmbryoMaker to explore the morphologies they can develop from very simple blastula-like initial conditions. EmbryoMaker is a mathematical agent-based model of development that can simulate any gene network, all known cell behaviours (division, adhesion, etc.), cell signaling, mechanical interactions, and the morphological transformations arising from all those. We found that cell division is the largest contributor to developmental instability. Cell divisions distort the borders of the territories (i.e. groups of cells with common gene expression) that send morphogens or activate morphogenesis. The activation of morphogenesis in territories with irregular borders leads to developmentally unstable morphologies. This is specially the case when territories are small and have high surface-volume ratios. We found that developmental stability can be highly increased if territories exhibit strong homotypic adhesion, if the cells in the border of the territory suffer planar cell contraction or if the cells between territories divide slowly. Moreover, we found that, although short range signaling can increase developmental noise by copying the irregular borders of territories, long range signaling and constant signaling can reduce noise in induced territories.