

QUANTIFYING THE ROBUSTNESS AND EVOLVABILITY OF A DEVELOPMENTAL SYSTEM

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Many developmental processes generate invariant phenotypes despite environmental or mutational perturbations. Such robustness is a fundamental biological property, yet its extent, limits and adaptive significance have rarely been assessed empirically. Here we tested how environmental variation and accumulation of spontaneous random mutation impact the developmental system underlying vulval formation in *Caenorhabditis* nematodes. In different environments, a correct vulval pattern develops with high precision but rare deviant patterns reveal the system's limits and how its mechanisms respond to environmental challenges. Key features of the apparent robustness are functional redundancy among vulval precursor cells and tolerance to quantitative variation in Ras, Notch and Wnt pathway activities. These environmental responses and the precision of the vulval patterning process further vary within and between *Caenorhabditis* species. To quantify how developmental precision responds to mutational perturbations, we used a set of mutation accumulation (MA) lines derived from two *C. briggsae* and two *C. elegans* genotypes. Developmental defects and variants increased after MA treatment for all tested genotypes, yet the type and proportion of the mutationally induced variation varied among genotypes. Thus, the mutability of this developmental system evolves, so that the mutationally induced phenotypic space is biased depending on the genetic background. Since the frequency of developmental defects and variants in MA lines is consistently higher than the one observed in various genotypes of natural populations, selection likely acts to maintain the robustness of this developmental process.