biologically suspect measure might well make one parameter seem less important than another. Thomas *et al.* measured isolation simply as the distance to the nearest suitable habitat patch. A better measure would reflect the total number of individuals likely to immigrate to this site from existing local populations anywhere in the system, and such a definition might further emphasize the importance of isolation [2]. Second, the relative importance of size, isolation and quality will depend on the specifics of the system. Size will have a larger effect in a system where patch size is heterogeneous compared with a system where all patches are approximately the same size. Third, the importance of habitat quality will probably vary with geographical location. The effect of habitat quality is generally assumed to be accentuated in populations near the edge of the species range. Nevertheless, habitat quality can usefully be thought of as a third parameter in metapopulation dynamics. Its inclusion can add realism to metapopulation modeling, which is vital for the conservation of our rarest species.

1 Thomas, J.A. *et al.* (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc. R. Soc. London B Biol. Sci.* 268, 1791–1796
2 Moilanen, A. and Nieminen, M. Simple connectivity measures in spatial ecology. *Ecology* (in press)

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The rise of the Aristotelean worms

Most developmental research focuses on a few model organisms, among which the nematode *Caenorhabditis elegans* is particularly prominent. Until recently, *C. elegans* was viewed as the ultimate deterministic organism, because there is a virtual absence of variation in cell number (eutely). However, Azevedo *et al.* [1] in their 'Demise of the Platonic worm', previously showed that the 'platonic ideal' of a worm, where each individual faithfully represents the essentialist idea of the species, does not hold true for all nematodes. The authors reported that, in the epidermis, the variance in cell number between individuals of a species increased with the mean cell number in that species.


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In a new article [2], Azevedo and Leroi report that the variability in some supposedly eutelic taxa is not unusually low, and that the relationship between cell number variation and mean cell number generally follows a power law with an exponent of 2 across a wide range of multicellular taxa. They use stochastic branching processes to model the way in which variation builds up in a lineage and convincingly argue that the relationship between cell variability and cell number must be maintained by selection. In another new article, Delattre and Félix [3] report variability in vulval cell lineages in several strains of *C. elegans* and of its close relative *Oscheius* sp. CEW1, and demonstrate that this variability is affected by several loci. Thus, lineage variability can even evolve over short evolutionary timescales.

These studies are important for several reasons. First, they provide a solution to the paradox that the *C. elegans* nematode model displays no developmental variation, whereas there is variation in development among nematode species. The current results no longer exclude a standard neo-darwinian scenario where the gradual divergence of a developmentally polymorphic population can lead to species differences. Second, these studies dispel the notion that *C. elegans* can serve as the platonic model for all nematodes. Finally, these studies provide a framework for unraveling the genetic mechanisms underlying developmental stochasticity. It is perhaps ironic that animals known for their invariance should provide materials for a better understanding of the developmental basis of phenotypic variability. This would really please Aristotle. In his view, knowledge comes from understanding and classifying variation in the empirical world.

1 Azevedo, R.B.R. *et al.* (2000) The demise of the platonic worm. *Nematology* 2, 71–79
2 Azevedo R.B.R. and Leroi, A. (2001) A power law for cells. *Proc. Natl. Acad. Sci. U. S. A.* 98, 5699–5704
3 Delattre, M. and Félix, M-A. (2001) Polymorphism and evolution of vulval precursor cell lineages within two nematode genera, *Caenorhabditis* and *Oscheius. Curr. Biol.* 11, 631–643

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Searching for Pax in hydromedusa

Pax6 is a perplexing gene with a fundamental role in eye development in a wide range of bilaterian animals. The puzzling thing is that the eyes of all of these animals are entirely different: the compound eyes of flies, eyespots of flatworms, and lens eyes of vertebrates cannot be considered homologous in the usual sense. Yet *Pax6* is expressed in the early development of all of them, and the functional domains are so highly conserved that mouse *Pax6* can induce eye formation in *Drosophila* – and not only in the usual place. Expression of *Pax6* (either the fly gene or its mouse homolog) can turn on eye formation throughout a *Drosophila* embryo, resulting in flies with eyes on their wings, legs or antennae. Homeotic mutants such as these, where a whole structure is induced to develop in a novel location, have played a key role in the hypothesis that body plans in animals arose by discreet (and potentially very rapid) evolutionary processes, rather than by the slow plodding of classic darwinian gradualism. But how can the puzzle of homologous gene expression (*Pax6*) in nonhomologous structures (metazoan eyes) with a common function (vision) be resolved? One approach is to work out what *Pax6* was doing in the ancestor of all animals that now use it as a regulator of eye development.

Cnidarians could hold the key piece of this puzzle. One of the most basal groups in the animal kingdom, Cnidaria includes creatures with a range of eye types from simple eyespots to complex lens eyes. Earlier studies of sea nettles, hydra and corals identified cnidarian Pax-family genes (including *PaxA*, *PaxB* and *PaxCAM*), but found no clear homologs of *Pax6*. But these cnidarians either have no eyes or just simple eyespots, hence this new study

