Journal Club

Explaining a little is often a lot

Both ecology and evolutionary biology are often accused of being 'soft' sciences. When we try to predict something, all we will find is often random variation. Even when we do find a pattern, it will often seem blurred by strong variation. Yet, this fact is not necessarily due to poor theory or inadequate methods, but a property that is inherent in the things that we study. To make our science tractable to the general public, to our students and to ourselves, we need to appreciate the level of variability present in complex biological systems. This will not only involve the identification of different predictable sources of variation, but also some quantification of the general level of variation that is present. Quite simply, we need to know what blur to expect.

Anders Pape Møller and Michael Jennions [1] now give us the first sketchy outlines. They combined 43 earlier meta-analyses in ecology and evolution into a single mega-analysis, and asked what proportion of the total variation was explained by the original author's favourite factor. The answer was clearly 'not very much': on average, the factor of main interest only accounted for some 2.5–5.4% of the total variation in the material.

These results provide a crucial yardstick against which to compare both past and future results. Hence, just when we thought we were seeing double, we might have enjoyed the best view that we could ever hope for. But the paper also offers some vital baseline information when planning for future studies. If the effects that we are looking for are generally this small, it will take a lot of work to find them: several hundred samples might be needed before we stand a fair chance of detecting any typical ecological or evolutionary pattern. Vice versa, the authors suggests that many negative findings might be due to the absence of evidence rather than providing real evidence for the absence of an effect. Statistical power might be depressingly small in many studies. Ultimately, this implies that we will be much better off if we focus our limited resources on more substantial studies rather than scratch the surface of every phenomenon in sight.

1 Møller, A.P. and Jennions, M.D. (2002) How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* 10.1007/s00442-002-0952-2

Tomas Roslin
tomas.roslin@helsinki.fi

Complex simplicity

Organisms of a given species, particularly the wild type of that species, look very similar to one another. This occurs in spite of tremendous variation in the environments that the organisms are exposed to and genetic variation within the species. In 1942, Waddington coined the term canalization to describe this robustness of the developmental process to environmental and genetic variation. Although canalization has been demonstrated experimentally, the exact mechanism that gives rise to it remains unknown. However, stabilizing selection, whereby those organisms further away from the optimal (mean) phenotype are selected against, has often been implicated as an important requirement. This conjecture is supported by numerous mathematical models, which demonstrate that canalization does evolve in the presence of stabilizing selection.

Whilst admitting that stabilizing selection is sufficient to produce canalization, in a new paper Siegel and Bergman [1] question whether it is a necessary component. Instead, they conjecture that the complexity of the developmental regulatory network alone might result in canalization. To test this hypothesis, they modeled the developmental process as an interacting network of genes and their transcriptional regulators using standard population-genetic approaches. Individuals in an initial population were assigned a genotype (defined as the matrix of regulatory interactions) and the population was followed through time, with random mating, mutation and selection between the generations. Siegel and Bergman found that canalization, which they measured as insensitivity of the phenotype to mutation, occurred even in the absence of stabilizing selection. More interesting, however, was that the degree of canalization was related to the complexity of the developmental network: more complex networks were more resistant to phenotypic change.

The implication of this result is that it is the complexity of the developmental process itself and not stabilizing selection that is the more proximate explanation of phenotypic stability. Stabilizing selection, however, still has an effect. Siegel and Bergman found that the time taken to evolve canalization decreased slightly with stabilizing selection. As the authors themselves admit, the model they used, although biologically realistic, is naturally overly simplistic. Complicating factors, such as a more realistic mutational model, including recombination, different selection regimes and modeling environmental variation need to be investigated. However, the results expand recent theoretical and experimental findings into the existence of robust networks (e.g. body segmentation in *Drosophila*) and how such networks are resistant to change. The importance of network dynamics, particularly in a developmental sense, has attracted increasing attention of late, and nicely brings together the fields of biology, development and computer sciences. Continued research in this area will undoubtedly yield many more surprises.

1 Siegel, M.L. and Bergman, A. (2002) Waddington's canalization revisited: developmental stability and evolution. *Proc. Natl. Acad. Sci. U. S. A.* 99, 10528–10532

Olaf R.P. Bininda-Emonds
Olaf.Bininda@tierzucht.tum.de

http://tree.trends.com 0169-5347/02/$ – see front matter