homogenization – testing of a mechanistic model using fish faunas. *Ecology* (in press)
6 Rahel, F.J. (2000) Homogenization of fish faunas across the United States. *Science* 288, 854–856
7 Marchetti, M.P. *et al.* (2001) Homogenization of California's fish fauna through abiotic change. In *Biotic Homogenization* (Lockwood, J.L. and McKinney, M.L., eds), pp. 259–278, Kluwer Academic/Plenum Publishers
8 Taylor, E.B. (2004) An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. *Can. J. Fisheries Aquat. Sci.* 61, 68–79
9 Olden, J.D. *et al.* (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19, 18–24
10 Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*, Methuen

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Book Reviews

A mania for modules

Modularity in Development and Evolution by Gerhard Schlosser and Günter P. Wagner. Chicago University Press, 2004. £63.00/£24.50 hbk/pbk (600 pages) ISBN 0226738531/0226738558

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Abstract nouns – 'hierarchy', 'connectivity', 'evolvability', 'complexity' to name four – are becoming increasingly popular as evolutionary developmental biology tries to find its theoretical feet. With Gerhard Schlosser, an amphibian developmental biologist, Günter Wagner has brought together a stellar team of contributors to discuss the abstract noun *du jour*, 'modularity.'

In *Modularity in Development and Evolution*, we can read contributions from 42 authors, many of them distinguished, about topics as diverse as basic helix–loop–helix transcription factors, data-mining genome-wide expression data, vertebrate limbs, nematode vulvas and *Wolbachia* symbionts. Unsurprisingly, all authors agree that modularity is very important to development. The question is: what do they mean?

The answer is: many different things. The editors make a brave attempt to keep matters under control by defining modules as structures or processes composed of tightly integrated parts, whilst being relatively autonomous from their surroundings. For developmental geneticists, modules are therefore groups of proteins that work together to specify cells [e.g. the Notch–Delta–Su(H), pathway]. For a quantitative geneticist, modules can be seen in the distribution of the pleiotropic effects of quantitative trait loci, which control various morphological traits. Developmental neurobiologists point to embryologically and functionally distinct units of the central nervous system, whereas a nematode geneticist points to cells. Bioinformaticists see modules in 'synexpression groups' – clusters of co-ordinately regulated genes visible from expression profiling studies; dynamic systems modelers see them as networks of genes necessary and sufficient for carrying out a particular function; a complexity theorist sees them in basins of attraction in random boolean networks. And this is only a partial list.

The sheer ubiquity of modular things, whatever those happen to be, suggests that modules matter to development. Having said that, one has the feeling that many contributors are cherry-picking the data. They are looking for, and finding, modules whilst ignoring non-modules. The problem seems to be that the modularity of things is, as the editors point out, a matter of degree. However, there is no formal theory of modularity and, in the absence of that, no consensus about how to measure it. The result is that we are invariably given the history of a case rather than a sense of its distribution. This is a natural history of modules.

What about their evolution? As with more mundane attributes that organisms might have, say, parental care or wings, evolutionary biologists want to know several things about them. Why do modules exist? Are they the result of natural selection? Or can mutation and drift explain their presence? If selection, what kind of selection? We also want know how they evolve. If a module is found in *Caenorhabditis elegans*, is it also found in another nematode species? A fruit-fly? Humans? Are modules more conserved than non-modules? Has modularity – like complexity – increased over the course of evolution?

These are important but difficult questions, and the contributors give a diversity of answers. Taking the last set of questions first, (how do modules evolve), it seems that sophisticated comparative studies of the evolution of modules are some way off. This is not a criticism: such studies need lots of data, which hardly exist outside of a few model organisms – but they will surely come. Why do modules exist? Some contributors seem to view modularity as an emergent property of genetic networks. Others suggest that developmental modularity evolves for its variational properties – it enables organisms to be more resistant to environmental or mutational perturbations. The split here is analogous to the Wright–Fisher dispute over dominance. Others again, suggest that modules permit evolvability (i.e. the production of heritable, selectable, phenotypic variation). This is a clade-selection argument – with all the weaknesses of such arguments. Many contributors hedge their bets by citing some or all of the above without considering the matter too deeply. But more careful discussions can be found in at least two papers. Force, Cresko and Pickett argue that 'genotypic modularity' – the use of genes in particular places and times independently of other genes – can increase simply as a consequence of

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mutation and drift. It's a lamentably jargon-ridden paper, but the ideas are important. Turning to selectionist arguments, Wagner and Mezy give an illuminating account of the weaknesses of classic modifier-selection arguments to account for 'variational modularity' – modules detectable from patterns of genetic covariance – and suggest an interesting solution.

You should buy this book. The individual papers alone are excellent. That by Von Dassow and Meir about modelling the segmentation network (a favourite of mine) is so richly and subtly suggestive that it will surely become a classic. Second, the outlook expressed by the contributors who, after all, seem to be studying very different things, is remarkably similar. This, more than anything, gives the book a real unity and, more importantly, this reader the sense that a general, formal, theory of development is in the offing. Modules are only a part of that theory, but they are surely an important part of what it might contain.

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Modelling subdivided populations

Genetic Structure and Selection in Subdivided Populations by F. Rousset. Princeton University Press, 2003. £26.95 pbk (288 pages) ISBN 0 691 08817 9

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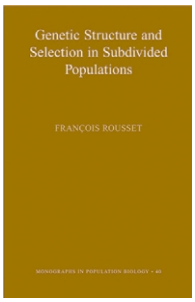

How to model evolution in a group of populations connected by immigration and/or local extinction and recolonization is one of the most formidable challenges for theoretical population geneticists. Success in meeting this challenge is crucial for providing a conceptual framework for tackling many of the problems in contemporary population genetics and evolutionary biology, particularly the interpretation of the rapidly increasing amount of data about molecular variation in natural populations. In *Genetic Structure and Selection*, François Rousset provides a detailed overview of both classic theory and many recent developments, especially those contributed by the author and his associates.

Rousset first presents the basic theoretical principles of selection and drift, developing the fundamental mathematical machinery for describing genetic relationships among individuals and populations in terms of the concept of identity by descent (IBD). Rather idiosyncratically, he treats this in terms of an infinite alleles mutation model, defining two alleles at a locus as being IBD if they are descended from a common ancestral allele without experiencing a mutation to a new allelic state. The more usual approach is to define IBD in terms of an ancestral 'reference' population, in which all alleles at a locus are deemed to be distinct, and descent from this population is traced without regard to mutation. There is a very brief discussion of why Rousset believes his approach to be superior.

He goes on to discuss neutral variability in the classic island and stepping-stone models in terms of his IBD concept, recovering the standard results of Maruyama and Kimura and Weiss. He also presents a more general framework for representing neutral evolution in structured populations, with a brief introduction of the important concept of separating events into those that occur on 'fast' and 'slow' timescales, respectively. This can be used to remove some of the complexities of modelling demographically and geographically structured populations.

Rousset also deals with selection in subdivided populations, providing a general but complex methodology for kin selection and ESS theory. This is based largely on work by the author and his colleagues, and represents the most innovative part of the book. Rousset then returns to problems of genetic drift, which are explored in the context of different measures of effective population size, including the effects of demographic as well as geographic structure. In addition to purely neutral variability, Rousset discusses the difficult problem of the fixation probability of a mutation subject to selection in a subdivided population, using a heuristic approach based on diffusion equations, which seems to work well in practice. This might be somewhat confusing to the reader, because he had previously treated the calculation of an ESS in terms of fixation probabilities, without indicating how to determine them in a subdivided population. In fact, the approach actually used to calculate an ESS does not really use fixation probabilities, but instead uses the expected numbers of copies of an allele transmitted to future generations.

Identity probabilities play a key role throughout this book, a testimony to the power of a concept independently invented over 60 years ago by Malécot and Cotterman. Although Rousset relates identity to the coalescent process, very little direct use is made of the coalescent framework, which might surprise readers conversant with the recent literature. Rousset barely mentions the fundamental property of the coalescent: describing the probabilistic properties of gene genealogies, onto which different types of mutational process can be overlaid to generate predictions for different types of genetic marker. Its great utility in predicting the properties of samples of

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