Theory of speciation: filling an empty hole

Fitness Landscapes and the Origin of Species by Sergey Gavrilets, Princeton University Press, 2004. US$99.50/£65.00 hbk, US$39.50/£26.95 pbk (432 pages) ISBN 069111983X/0691117586

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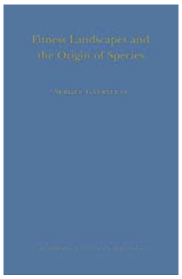

Although speciation research is an active field, there have, until now, been notably few books for researchers to keep up-to-date with this broad subject; suddenly, we're spoilt for choice [1–3]. Gavrilets' book is a timely contribution: an overview, critique and synthesis of the massive body of population genetic theory on speciation. It conveys the excitement of current work, the depth of literature lost in the pre-database black hole, while also presenting an idiosyncratic and challenging view of the subject.

The core of *Fitness Landscapes and the Origin of Species* is a detailed treatment of a wide range of models, organized by underlying mechanism. Most speciation models focus on the plausibility of single scenarios, and the book is refreshing in that it makes use of analytical results to compare the likelihood of different models and the patterns of speciation that they predict, rewarding the reader with several important insights. The mathematics will prove heavy going for 'non-model' readers as, in places, it is difficult to track the details of the many models on display. But for speciation researchers, it is mostly well worth the effort. In each chapter, the author cites biological examples of the scenario envisaged and a summary of main conclusions. Importantly, *Fitness Landscapes and the Origin of Species* also provides a good introduction to biological reality for non-biological theorists (we all know one).

Some people might be put off by the title of *Fitness Landscapes*, assuming allegiance to peak shift models of speciation or to abstract physics. Don't be – the book is about speciation. The metaphor of fitness landscape is largely optional and the book stands alone without it. Gavrilets' concept of holey landscapes is there, together with a fascinating section on RNA fitness landscapes, but this seems a sideline from the main task of comparing and contrasting speciation models. The metaphor is returned to later more as 'topping' than as the main impetus of the models. Peak shift models *sensu* Wright are dismissed on the weight of theoretical evidence. But, overall, the new, more realistic metaphor seems to have caught on in the evo–devo and adaptive dynamics literature more than in speciation studies.

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One of the most forceful messages is that sympatric speciation is hard to achieve, much more so that are either allopatric or parapatric speciation. This is hardly new, but the importance is that Gavrilets bases his conclusions on analysis of the same models used by proponents of sympatric speciation to feed their addiction. The first models of sympatric speciation emerged during the 1960s, but top-impact journals still publish models doing little more than showing plausibility. Gavrilets asks how likely is it that conditions would be met and how more likely is speciation in those conditions when gene flow is restricted? The answers are unlikely, and that speciation by sympatric-type models is much more probable with geographical restriction to gene flow: speciation would tend to 'crystallize' around a barrier to gene flow. This will be unpopular with contrarians who are dissatisfied with allopatric speciation, but, alas, it is time to face up to the theory and evidence. Although it is without doubt hard to demonstrate conclusively what conditions prevailed at the initial stages of speciation, it is nonetheless easy to imagine a world that is more sympatric than ours – every lake could have endemics such as the Nicaraguan crater lake cichlids [3] and every species could live in close harmony with its immediate sister. Fortunately, interesting genetic and ecological mechanisms still apply in non-sympatric scenarios.

All the classic speciation models are on show, but the most challenging parts are where Gavrilets pushes these models to address the environmental setting of speciation. Speciation is caused by a change in environment, whether it is the origin of new geographical isolation or the onset of divergent selection in an ancestral population. To date, most models have focused on population genetics and have treated the environment in fixed or simple terms. The result is that models begin with a single population and finish with two or more daughters, but there is no dynamic for how the conditions can later arise to enable further speciation in the daughters. Gavrilets attempts to ask such questions, for example in his deme-based models of parapatric speciation or in a section on the origin of higher taxa. Although the biological reality of specific models can be criticised (certainly the origin of higher taxa would benefit from a phylogenetic perspective), the important point is that we need such models.

There remain controversies in the genetics of speciation, many touched on in *Fitness Landscapes and the Origin of Species*, but the overall impression is that population genetics for a given setting is largely solved.

What we need now are dynamic models of how environmental changes favouring speciation interact with population genetics. Taking a realistic population in a realistic environment, what are the dynamics of different mechanisms of speciation? Only then can we predict diversity patterns and estimate speciation parameters from real observations. This book is a major stimulus for such efforts.

References

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