

Integrating ecology and genetics in speciation research

Ecological Speciation by Patrik Nosil, Oxford University Press, 2012. US\$43.74/£29.95, pbk (280 pp.) ISBN 978-0-19-958711-7

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The origin of species is one of the most complex processes in evolution, and unraveling its mechanisms requires integrating across key biological disciplines. *Ecological Speciation's* stated goal is the integration of the ecological and the genetic literature on speciation. To achieve this, the author cuts a slice out of the larger pie of the speciation literature;

this is 'ecological speciation'. The premise that divergent adaptation plays a central role in speciation dates back to Darwin [1], but the term 'ecological speciation' rarely appeared in the literature until late in the 1980s. The birth of the concept was perhaps an answer to the dearth of ecology in the speciation research of the 1970s and early 1980s, a time during which much of evolutionary biology lived in divorce from ecology. In those days speciation theory was preoccupied with the geographical modes of speciation. The birth of ecological speciation marked the beginnings of a transition towards emphasis on mechanisms. The use of the term increased exponentially following a number of key publications around the turn of the century [2,3]. A review of the field is very timely.

So what is ecological speciation, and what is it not? Part 1 of the book introduces tests to distinguish ecological from non-ecological speciation. Adopting Mayr's biological species concept, Nosil defines speciation as the evolution of reproductive isolation. Ecological speciation then is when this is driven by divergent ecological selection. A central tenet of the book is the idea that local adaptation is the first step in ecological speciation and divergent selection a major form of reproductive isolation. Mechanisms that do not involve divergent ecological selection are considered alternatives to ecological speciation. This definition has been criticized [4], but I like its utility. It does, however, have some shortcomings.

One might take issue with equating divergent selection with reproductive isolation, and local adaptation with (the beginnings of) ecological speciation. Does reproductive isolation arise automatically as a consequence of divergent selection? It might do where niches are discrete, such as in insect host races [5], but it seems far less obvious where resources vary on a continuous scale [6]. Another consideration is that because local adaptation is much more widespread than speciation, and because the genetics of local adaptation tend to be much simpler than those of the complete process of speciation, the key question becomes when and how divergence proceeds well beyond local

adaptation. Different mechanisms of population divergence are of course also not mutually exclusive. It is possible, even likely, that coincidence of divergent ecological selection with other sources of incompatibility may fuel ecological speciation or be required for its completion. Would this no longer be ecological speciation?

The book is effortless reading, rich in verbal and conceptual models, hardly any equations. The author excels in giving brief and clear explanations, summary tables allow readers to connect to the primary literature. The book follows a logical path. After introducing predictions and tests of ecological speciation, its three main components are reviewed: sources of divergent natural selection, forms of reproductive isolation, and genetic mechanisms to link the two.

What is known now is that ecological speciation can happen in many geographical settings, though perhaps most easily when rates of gene flow are low. Sources of divergent selection are known too. Forms of reproductive isolation are sometimes known. The genetic mechanisms that link the two, that is pleiotropy or linkage disequilibrium – well appreciated in theory – remain little known in practice. Some genes are known that affect adaptation, but none of these genes have yet been demonstrated to unequivocally affect reproductive isolation. Thus, 'ecological speciation genes' are yet to be demonstrated. What is perhaps even more surprising is how little is known about the causal relationships between gene flow and adaptive divergence. The reason seems to be that almost all tests of ecological speciation are either correlative and indirect or from laboratory studies. Nosil suggests manipulative field experiments as 'the final frontier' in tests of ecological speciation that would help closing some of the current knowledge gaps.

Among the other things that I found remarkable was that the classical isolation mechanisms, intrinsic incompatibilities and sexual isolation, have currently limited evidence supporting them in the ecological speciation literature. Does this imply that these usually evolve only after speciation is (nearly) complete, or that ecological speciation studies often deal with the early initiation of a process that may or may not result in speciation? What surprised me too is that no single case seems to be known of ecological speciation by a one-allele assortative mating mechanism, which theory predicts is the easiest way to get ecological speciation [7].

The chapter on the genomics of ecological speciation is short but does achieve its goal to offer a glimpse of what the future might hold, including research on effects of the genomic arrangement of 'speciation genes', the genomic

distribution of the effects of divergent selection, and an emerging field of ‘experimental genomics’ [5]. More on the ecological side, evidence that gradual transitions occur from populations, to ecotypes, to species, is still scarce and an interesting question arises whether intermediate stages can be quasi-stable, or if feedback loops cause divergence to either quickly proceed to completion or to collapse again. The roles of dimensionality of ecological shifts and more multifarious versus stronger selection are still unresolved. A related question is whether divergence in many dimensions may result in ‘holey’ rather than rugged adaptive landscapes, where drift could become an important driver of diversification besides selection [8]. Studies reconstructing adaptive landscapes from genome wide measures of selection might address this question in the future.

Ecological Speciation leaves little doubt that knowledge of ecology is essential to understanding the origin of species not just in adaptive radiation, but indeed more generally [9]. The book ends on a hopeful note, ‘where gaps in our knowledge exist, it is often clear what needs to be done and the tools to do so are generally available.’ And this is

perhaps the biggest strength of this book – it provides for a springboard for future discovery: a must read for students of speciation at any stage of their career.

References

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