Evolutionary biology

Splitting in space

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Disjunct distributions of closely related species are not necessarily the outcome of passive fragmentation of populations. Instead, they can be the consequence of speciation within a population.

Until recently, the overriding credo for explaining how new species are formed has run as follows: first, a population of organisms splits into several subpopulations; once isolated from other members of their own kind, these subpopulations become adapted to local conditions; so, over millions of years, their descendants evolve into new species. This is 'allopatric speciation', a concept in which spatial separation comes first and genetic divergence follows, and which has dominated biological thinking for many decades. The alternative, 'sympatric speciation', in which new species are created within a single population, has long been seen as a heresy — to the extent that young biologists would risk their careers if they proposed that such a mechanism could occur[1].

Over the past few years, however, modelling work[2–4] has shown that spatial separation of populations is not a prerequisite for genetic splitting. Doebeli and Dieckmann (page 259 of this issue[5]) now go even further. They propose that spatial separation is a secondary consequence of adaptive genetic divergence under sympatric conditions. In other words, splitting of a population in space can follow genetic splitting within it.

One of the strongest arguments against sympatric speciation, namely that there are no convincing mechanisms for genetic separation in sympatry, has already been addressed in the previous models[2–4]. These models solve the problem of preventing gene flow between differently adapted genotypes, a necessity if speciation is to occur, by giving the individuals an active role in choosing their mates. This is called assortative mating or mate choice, and is a well-documented phenomenon in natural populations. One model[3] suggests the parallel evolution of ecological adaptations and signals that enable individuals to recognize mating partners with genetic adaptations that are similar to their own. The other two[2,4] show that the evolution of the signals, and specific mate choice or sexual selection alone, can in themselves lead to genetic splitting.

But although there are field studies that support these models[6,7], most biologists still see sympatric splitting only as an interesting exception. This is because there is a second argument in support of allopatry: common experience shows that closely related species are usually spatially separated. If one takes this pattern as a reflection of the process, one inevitably arrives at the conclusion that, although sympatry is possible, allopatry is the norm. But this is exactly the point at which the new work will change the prevailing view.

Doebeli and Dieckmann[5] base their model on evolutionary branching[8,9], which has already shown its usefulness for understanding the sympatric splitting process[3]. Evolutionary branching describes a process, known as 'disruptive selection', under

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conditions of 'frequency-dependent competition'. In short, this means that in any given population that becomes adapted to a particular ecological niche, there will be increasing competition among those individuals that are best adapted simply because they are the most frequent ones. The consequence is that their genotypes have a lower probability of being transmitted to the next generation than the less frequent genotypes, which use only parts of the resource spectrum of the given niche. This leads to disruptive selection for specialization and consequently to the population's splitting into two new species with differential adaptations.

Doebeli and Dieckmann now add a spatial component to this process by considering an uneven distribution of resources caused, for example, by environmental gradients in temperature, nutrients or altitude. In this situation, local adaptation along the gradient increases the chance that interactions occur between similar individuals, and hence increases the strength of frequency-dependent selection. This leads to two surprising results. First, a sharp geographical separation of populations is generated during the splitting process, although the resource distribution remains continuous. Second, the ecological and genetic conditions under which this occurs are even easier to fulfil than in the previous model without the spatial component. Most interestingly, environmental gradients with intermediate slopes work better than gradients with steep slopes, a result that is in complete contrast to predictions of classical models that are based on allopatric concepts.

Is this all only modellers' fantasy? As yet there is no direct evidence to confirm the predictions of the model, but there are studies pointing in the right direction. For instance, Ogden and Thorpe[10] have looked at the genetic differentiation of lizard populations on the Caribbean island of Martinique. By sampling the populations along carefully controlled transects, they showed that there is a sharp reduction of gene flow along a transect covering habitats at different altitudes, but not along two control transects within homogeneous habitats. Intriguingly, they also find no reduction of gene flow across an old allopatric split, indicating that habitat ecology is more important for gene flow than historical contingencies. Thorpe and Richard[11] previously drew a similar conclusion in a comparable study of lizards on the island of Tenerife.

It is satisfying that the inclusion of more realistic conditions into an abstract model of sympatric speciation leads to results that explain natural patterns that have long been used as arguments against sympatric speciation. This shows that the common experience that closely related species are usually spatially separated cannot be taken as direct evidence for the prevalence of allopatric speciation. But then, science has a habit of showing that common experience is not always a reliable guide to reality. ∎

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