Speciation without isolation

Tom Tregenza and Roger K. Butlin

There is abundant evidence that new species can arise when a population of organisms is split into isolated elements. The occurrence of sympatric speciation — speciation without isolation — is much more contentious but is now set on firmer theoretical ground.

The rise of biomathematics, which led John Maynard Smith to say, "if you can't stand algebra keep out of evolutionary biology"[1], has been a runaway success. In many fields, empiricists continually struggle to keep up with and verify the assumptions and predictions of modellers. An exception is the famously contentious topic of sympatric speciation — the process by which new species arise from coexisting as opposed to geographically isolated populations. There is growing evidence, particularly from lakes full of closely related fish species[2], that sympatric speciation does occur in nature. But models of the phenomenon have stubbornly concluded that evolution of sexual isolation without spatial isolation seems very unlikely.

At first glance, sympatric speciation looks straightforward. If a lake contains two potential resources — say, large or small prey — then large or small predatory fish will do well while medium-sized fish will be at a disadvantage. This disadvantage to intermediates, termed 'disruptive selection', creates pressure for divergence into two populations of distinct ecological types.

In sexual populations, the stumbling block preventing sympatric speciation is that mating between divergent ecotypes constantly scrambles gene combinations, creating organisms with intermediate phenotypes (physical characteristics). This mixing can be prevented only if there is assortative mating, in which pairings between similar individuals are more common. With disruptive selection, this pairing pattern is selectively favoured, because it reduces the production of offspring that are less well adapted to their environment. But there is a barrier to the evolution of assortative mating — recombination, the shuffling of genes during gamete formation, which means that genes for mating preference and ecotype (size for instance) may get mixed up whenever an occasional mating between different types occurs. This creates individuals with a preference for the opposite ecotype, increasing gene flow between types and opposing speciation.

Modellers have sought to duck this problem by assuming one of two things — either that the genes responsible for ecological traits and for mating preferences are so close together on a single chromosome that they are only rarely mixed up by recombination[3], or that a single gene could both code for the trait and create a preference for partners with that trait. These are plausible assumptions for some situations, such as an insect shifting to a new host plant where it also mates[4]. But in general they are not.

Two new theoretical treatments by Kondrashov and Kondrashov[5] (KK, page 351 of this issue) and Dieckmann and Doebeli[6] (DD, page 354) address these difficulties. Both present models in which there are several separate genetic loci for ecological traits and mate preferences (see Box 1 overleaf for details). With these more realistic assumptions, both predict that sympatric speciation can occur without very strong selection against intermediate forms.

There are two variants of the KK model. In the first, mating probability depends on how similar two individuals are for a single marker trait (such as colour); in the second, it depends on a match between male trait and female preference. In the DD approach, mating probability is determined by either the ecological trait or a marker trait, with these loci exerting their influence through a separate set of mating loci. In all of the models, selection increases associations between ecological and marker traits, leading to sexual isolation between ecologically distinct populations (Fig. 1).

In the KK model, disruptive selection is assumed to favour the most extreme phenotypes, regardless of their absolute values. However, this does not fit with the example they give of selection due to two distinct
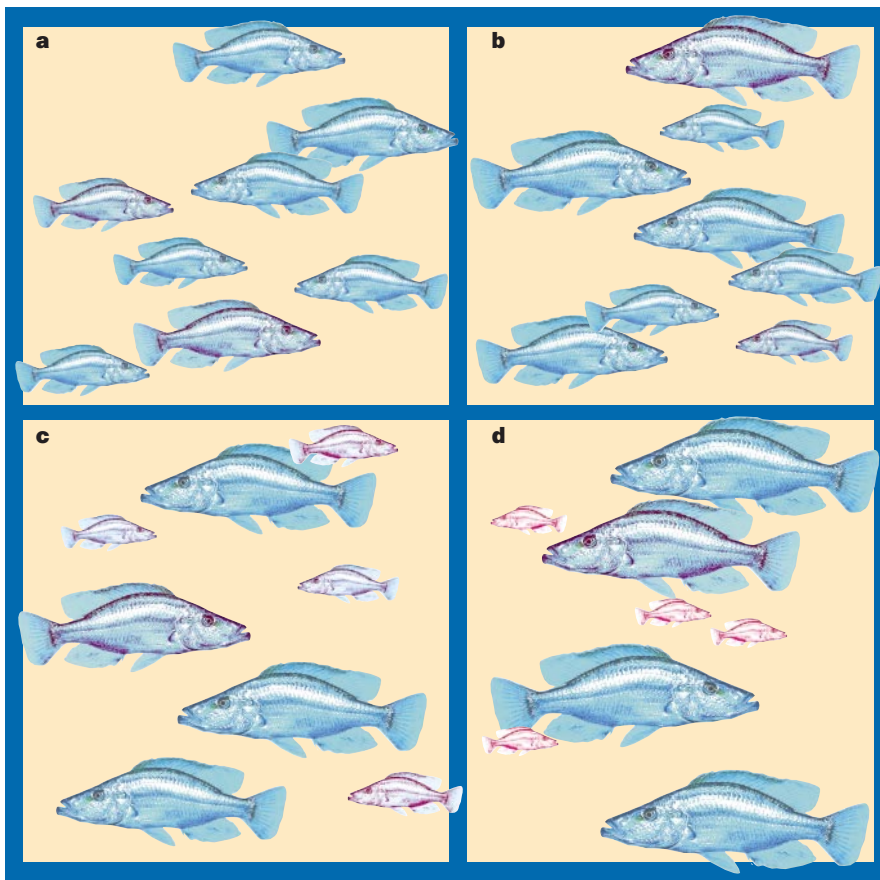

Figure 1 **Sympatric speciation according to the KK model[5]. The population is initially uniform for both ecological traits (size) and mating traits (colour), but contains genetic variation for both traits.** a, **The population rapidly evolves to intermediate size.** b, **Disruptive selection creates divergence in ecological traits.** c, d, **This in turn creates selection for assortative mating, increasing variation in colour, and increasing association between colour and size. The process is similar in the DD model[6], except there is greater initial variance in colour, and colour and mating traits diverge at the same time. Unlike previous models, positive covariance between preference and traits develops rapidly despite maximum recombination between genetic loci. The more realistic assumptions[5,6] about genetic architecture increase the theoretical likelihood that sympatric speciation can occur.**

Box 1: Genetic architecture and modelling approach

Although the models discussed here[5,6] agree on the headline prediction that disruptive selection can drive sexual isolation, and result in sympatric speciation, they differ fundamentally in how they arrive at this conclusion. The DD model allows stochastic variation in genetic composition to create associations between preferences and traits. By contrast, the KK model is deterministic, and simply assumes an initial low level of linkage disequilibrium – a greater-than-chance tendency for preferences and traits to be inherited together.

This difference changes the models' predictions about the effect of the number of genetic loci underlying each trait.

In the DD model, the effect of number of loci is considered in terms of its effect on genetic drift. If more loci are involved, speciation tends to take longer because drift is weakened, giving fewer opportunities for chance increases in association between ecological and mating traits to trigger selection for assortative mating. In the KK model, the parameter considered is the strength of disruptive selection required to drive divergence. In this case, larger numbers of ecological loci increase the chances of speciation because they increase the production of disfavoured intermediate phenotypes. The numbers of marker loci have the opposite effect, as fewer marker loci mean more extreme (and hence isolated) marker phenotypes. These differences make a direct comparison between the models' predictions impossible, which is a pity: it is important to know how robust the predictions of the models are because they point to ways of identifying cases of sympatric speciation. **T. T. & R. K. B.**

resources. For instance, if a lake contains large and small food items, and fish are initially all small (as in the KK model), then slightly larger individuals will be less efficient at eating small prey, but still hardly any better at eating large prey. Therefore, with two resources, selection does not simply favour the smallest and the largest individuals. It will favour both extremes only if the population begins at an intermediate size, or if there is competition between individuals.

In the DD model, disruptive selection explicitly arises from competition for a single resource — a potentially more common ecological situation. The resource is assumed to have a unimodal distribution such that its carrying capacity is highest when the entire population has a particular phenotype. Selection leads to the phenotype of all individuals initially converging on this point. This provides an explanation for the nagging problem in other models of how the initial population comes to be in a state in which all phenotypes are intermediate and adaptation to the environment is suboptimal. As the population converges on the resource maximum, competition between similar individuals creates selection in favour of those with a divergent genetic make-up that use slightly less abundant resources but experience a more than compensatory decrease in competition. With assortative mating, this process eventually leads to 'evolutionary branching'[7] — two distinct and reproductively isolated phenotypes are selected despite the resource being unimodal.

An assumption of disruptive selection generated by competition is that there are no

other species that might tend to counter divergence within the focal species through increased interspecific competition. If an absence of other competitors is indeed important, sympatric speciation resulting from competition may be most likely in new, empty habitats. This fits with examples from crater lakes[8]; these lakes were initially empty, but appear to have been colonized by a single

species of fish which has subsequently given rise to a number of species.

As well as being likely to convince many sceptics of the theoretical tractability of sympatric speciation, these new models apply equally to the other contentious example of selection leading to speciation. 'Reinforcement' is an increase in pre-mating isolation between two divergent groups, resulting from selection against hybrid offspring because they are less viable or fertile than their parents[9]. As with sympatric speciation, the main objection to reinforcement has been that recombination will break down the link between mating preferences and genes responsible for hybrid dysfunction. The fact that sympatric speciation can occur despite such recombination indicates that reinforcement may also have escaped its theoretical straitjacket[10]. □

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Materials science

Superhard ceramics

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In contrast to the polymer scientist, who has the privilege of calling upon an ever-expanding array of compositions from which to choose, the ceramic scientist has had to devote years of intensive research to the refinement of a relatively limited number of systems. So it is exciting news to hear from Zerr *et al.* on page 340 of this issue[1] that in one of these systems — silicon nitride — a new form of compound has been found. Moreover, the new cubic compound is potentially much harder than existing phases, offering considerable industrial scope for the material.

Silicon nitride[2] (Si_3N_4) has two long-established crystal forms, α and β. In both, the central silicon is linked to four surrounding nitrogens in a tetrahedral array (Fig. 1a). The different crystal structures are then distinguished by the ways in which the set of tetrahedra are linked to one another. In Si_3N_4 each tetrahedron is linked at each corner to

two others, conferring a greater degree of structural rigidity than for silicate systems where the tetrahedra (formed from silicon and four oxygens) are linked one-to-one at the corners.

In the ceramics community, Si_3N_4 has enjoyed an exceptional degree of attention largely because of its potential as a material for high-temperature heat engines. The excitement arises in part from its mechanical properties, such as greater strength and ability to resist mechanical failure when subjected to sudden temperature changes. It is also less brittle than many ceramics, owing to the way in which the crystalline grains in the material become acicular (that is, length ten times greater than width); the resulting interlinking improves the resistance to mechanical failure. Ceramics are traditionally prepared from powdered materials, and Si_3N_4 is no exception: the precursor material is shaped into a powder mass, which is then