

Figure 1 Superdiffusion in solid helium. a, Migration of crystal vacancies, and counterflow of atoms, around a stress-imposing wire in a solid crystal of helium, which allows the wire to move. b, Velocity of the wire as a function of temperature as observed by Polturak *et al.*¹, showing a peak at the temperature where 'superdiffusion' of atoms and vacancies occurs. This peak coincides with the temperature at which helium changes crystal structure, and is much larger than any such effect seen in metals (note that the ordinate scale is logarithmic).

softening of a particular kind of crystal vibration, or mode in the phonon spectrum⁷. Polturak's group thinks the same process causes the helium effect. The extraordinary magnitude of the peak in Fig. 1b is associated with the very low formation energy for crystal point defects in helium (~ 1 meV) compared with b.c.c. metals (~ 1 eV). This low formation energy for He suggests that both the concentration and the mobility of point defects, such as vacancies, might be greatly enhanced near the peak. Computer simulations by Polturak *et al.*³ suggest that the point defects responsible for the very fast diffusion may in fact be a type of interstitial structure in the crystal lattice rather than vacancies.

The acceleration of vacancy creep under a small stress (also called superplasticity by metallurgists) at a phase-transformation temperature is a well-established fact, but in metals the magnitude of such acceleration is nothing like that observed in helium. Polturak and colleagues² have evidence that the presence of ³He enhances superdiffusion in ⁴He by further reducing the point defect formation energy. So in isotopic mixtures, the magnitude of the diffusion peak at the transition temperature is even greater than that shown in Fig. 1b.

The significance of these studies in helium is the unprecedented degree of enhancement of point defect concentration and mobility at a phase transformation. These findings are also relevant to melting theory, in that a very high density of point defects combined with a softened phonon mode can lead to melting, by reducing the shear resistance near the transition to the point where the solid becomes mechanically unstable. In their latest work³, the authors suggest a feedback mechanism in which the point defects in helium soften the phonon (vibrational) spectrum, and this in turn enhances diffusion and creates more point

defects. This feedback mechanism, and a very high density of point defects to begin with, are crucial ingredients in producing a mechanical instability sufficient to generate melting: both are missing in rival theories of melting, of which there have been many over the years. □

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errata In J. Bland-Hawthorn's article "Clues to galaxy formation" (*Nature* **400**, 220–221; 1999) the image in Fig. 1 was not produced by the Virgo Consortium and was not published in ref. 12 as stated. The image should have been attributed to G. Kauffmann, J. M. Colberg, A. Diaferio & S. D. M. White, *Mon. Not. R. Astron. Soc.* **303**, 188–206 (1999), as part of the GIF project (http://www.mpa-garching.mpg.de/~jgc/sim_gif.html).

The source of the cichlid images used in the graphic accompanying Tom Tregenza and Roger K. Butlin's "Speciation without isolation" (*Nature* **400**, 311–312; 1999) should have been acknowledged as a photograph taken by Michael K. Oliver. The photograph of the species concerned, *Dimidiochromis compressiceps*, and others can be viewed at *The Cichlid Fishes of Lake Malawi, Africa* <http://www.connix.com/~mko/>

Daedalus

The insect plane

Aviation engineers look with envy on birds and especially insects. Their flapping wings lift and propel them far more efficiently than the fixed wings of aircraft. One reason is their ability to exploit the subtleties of stalling.

If the angle of attack of a wing is increased, it ultimately stalls, with sudden, disastrous loss of lift. No fixed-wing aircraft dare risk stalling. But an insect with oscillating wings can exploit an intriguing loophole in the laws of aerodynamics. Accelerated at a high angle of attack into the stalling regime, a wing takes a short while to stall. And until it does, it generates enormous lift. By speeding into stall and out again at each flap, an insect wing develops amazingly high average lift.

So Daedalus is inventing a non-steady-state aircraft wing. A conventional wing could never be made to flap, of course. But it might be covered with a flexible elastic fabric, and this could be flapped by a system of rapid repeated inflation and collapse. It might even be made to flap spontaneously in the slipstream, as a flag does in the wind. But the ideal solution is simpler still. Instead of flapping the wing or its surface, Daedalus plans to flap the airflow around it.

Cunningly, he will generate this non-steady airflow from a non-steady propulsive source, a pulse-jet of the type used to power the old V1 missile. Its primitive motor drew in air through a one-way valve, and mixed it with petrol vapour in its combustion chamber. When the chamber was full, a spark ignited the mixture. The valve closed, directing the propulsive blast out through the tail-pipe. The valve then opened and the cycle repeated. So Daedalus's new 'pulse-wing' aerofoil has a leading edge enclosed in cunningly shaped ducting, which acts as a long, thin pulse-jet combustion chamber stretching the length of the wing.

Each time the chamber fires, a sheet of hot gas blasts from the ducting, entraining the airflow round the wing. It speeds it up dramatically, and veers it upwards to put the wind into brief extreme stall, thus creating a sudden pulse of enormous lift. The craft is both propelled and held aloft by repeated pulses. To minimize noise and vibration, Daedalus hopes to drive his pulsed wing in a continuous, distributed manner. Each explosion will spread from the wing root out to its tip, by which time another explosion will be starting at the root.

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notoriously difficult to test. O'Connell and colleagues' proposal may, or may not, fit with the fossil and archaeological evidence, but possible tests include stable-isotope analyses to check for any dietary shift, and a search for residues of woodworking or starch grains on appropriate stone artefacts. Although the contemporary stone tools would not be obviously effective for hunting, they would have been adequate for preparing wooden digging sticks. *Homo ergaster's* body shape indicates that it is the first hominin to dispense with a large digestive tract, so its diet must have differed from that of its australopithecine predecessors, who, apparently, had a large gut like the living apes¹³. Moreover, *H. ergaster's* relatively small jaws and teeth are consistent with a diet requiring lower bite forces and less chewing. Wood and Collard¹⁴ and Wrangham *et al.*¹⁵ suggest that these changes are related to processing of food outside the mouth, through cooking. This proposal is also put forward by O'Connell *et al.*¹, who review the archaeological evidence for hominin-controlled fires.

The attraction of the foraging hypothesis is that it is the first attempt to link the nexus of morphological, life-history and cultural

changes that we see in the hominin fossil record a little less than 2 Myr ago. By playing down the role of meat eating at this stage in hominin evolution, O'Connell and colleagues' hypothesis raises the possibility that the increased body mass owing to foraging, combined with access to a more reliable source of meat, allowed the increase in absolute and relative brain size that was the next major innovation in human evolution.

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Cosmology

Clues to galaxy formation

J. Bland-Hawthorn

In 1977, Stephen Weinberg observed that “the theory of the formation of galaxies is one of the great outstanding problems of astrophysics, a problem that today seems far from solution”¹. Although the past two decades have seen considerable progress, many questions remain. Broadly speaking, the quest for answers has followed two paths: near-field cosmology (looking for clues close to home) and far-field cosmology (looking back in time (redshift) for the progenitors of modern-day galaxies). In their latest joint venture, Leo Blitz, David Spergel and their colleagues² propose that an important clue may have been in plain view — that is, in the near field — for almost 40 years.

We know through direct observation that the Universe was vastly hotter and denser in the distant past than it is today. As the Universe expanded it cooled to a point where atomic hydrogen distilled out of the primordial plasma. A vast literature of theoretical work, aided by supercomputer simulations, has concentrated on what happened next. Here we must acknowledge the primary role of dark matter in driving galaxy formation, as it accounts for more than 90% of the mass in the Universe. Although the nature of dark matter is a complete mystery, the consequences for galaxy formation are radically different depending on whether dark matter is ‘hot’ or ‘cold’ (or a mixture of both). We

now know that dark matter must be mostly cold in order to produce the small-scale structure we see today in three-dimensional galaxy distributions³.

The modern paradigm is that when the Universe was cool enough to form atoms, much of the dark matter existed in small clumps. As time progressed, gravity caused these clumps to cluster together to form bigger systems, and onwards to galaxies. Supercomputer simulations have become an essential tool for understanding how cosmic evolution progresses in a hierarchical universe⁴.

When looking at such simulations (Fig. 1) it is important to keep in mind our humble vantage point. We live on the outer reaches of a very ordinary spiral galaxy within the Local Group, a motley collection of 40 or more (mostly small) galaxies. Our Galaxy and the Andromeda Galaxy dominate this group, accounting for more than 80% of the starlight. The Local Group is but a small subset of a much larger complex of galaxies known as the Coma-Sculptor Cloud, which in turn forms a small part of the Local Supercluster⁵. Supercluster scales are the largest entities modelled in computer simulations, and extend over distances of several hundred million light years. In short, we find ourselves in a sparse environment, somewhere along one of the connecting bridges that join the dense clusters.

Although most of the activity associated with galaxy formation took place in the distant past, there are good reasons for believing that the outer reaches of galaxies are still in formation, at least in backwaters like the Local Group⁶. Many astronomers are tantalized by this possibility, not just because it may confirm our basic understanding of galaxy formation, but because of the chance to identify truly ‘primordial’ structures in the near field.

So where are these primordial building blocks? Blitz *et al.*² claim to have the answer. More than one-third of the sky is peppered with compact clumps of neutral hydrogen whose motions depart fairly radically from Galactic rotation. Discovered in 1963, these ‘high-velocity clouds’ (HVCs) have been the subject of wide-ranging speculation ever since. In the 1970s it became clear that a large fraction of HVCs fall along the Magellanic Stream, a thin band of gas encircling the Milky Way, which was presumably stripped from the Magellanic satellite galaxies⁷. After excluding these clouds, Blitz *et al.* argue that the motions of the remaining HVCs reflect the gravity field of the Local Group rather than our Galaxy. This puts their average distance at hundreds of kiloparsecs (1 kiloparsec = 3,262 light years), or far beyond the Galaxy. As a consequence, these clouds are typically 20 kiloparsecs and roughly 30 million solar masses of hydrogen in size, with potentially ten times more mass in the form of dark matter.

The Blitz *et al.* picture is very attractive because it unites ideas and observations that have been shelved for years. As early as 1966 Jan Oort⁸ noticed that the so-called virial

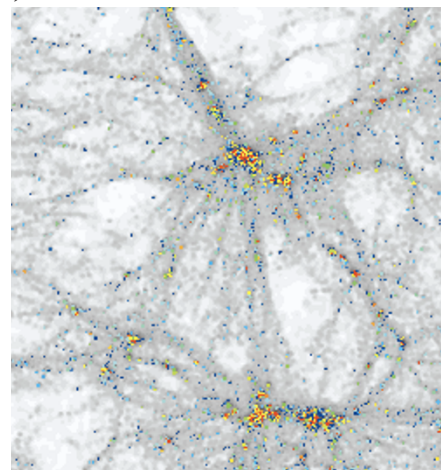


Figure 1 How the Universe might appear today, from a state-of-the-art N-body simulation by the Virgo Consortium¹². This thin slice is millions of light years across. The ‘cold dark matter’ clumps are shown in grey; red objects are galaxies consisting mostly of old stars; blue galaxies are still forming new stars at the present time. Blitz *et al.*² argue that clouds of gas and dark matter are galactic building blocks falling into the Local Group of galaxies to which our own Milky Way belongs.

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theorem, which relates the gravitational energy of an object to its kinetic energy, would place many HVCs outside the Local Group. For each cloud, radio observations obtain a spectrum of the hydrogen emission line at a wavelength of 21 cm. The total intensity of the line is directly related to the cloud's mass and distance. For a self-gravitating cloud, the intrinsic width of the spectral line is also related to the cloud's mass but has a different dependence on distance. Presumably the inferred masses are the same, in which case a crude 'virial' distance can be determined. This distance depends on a basic assumption that the clouds are held together by gravity, and therefore an independent distance estimate is called for.

One method is to look for bright sources with well-calibrated distances along the line of sight to a gas cloud. If the cloud produces absorption in the visible spectrum of the more distant source, but not in the spectrum of the nearer source, the distance to the HVC can be bracketed⁹. At present, this method has been applied only to background sources within the Galactic halo.

Another method has the potential to reach much greater distances. A spate of new surveys (for example, see ref. 10) reveals that HVCs along the Magellanic Stream are easily observed from visible emission lines of hydrogen. Whereas the radio spectrum is produced by neutral atoms, the visible spectrum arises from hydrogen ionized after absorbing ultraviolet photons. The latest observations (M. E. Putman and J. B.-H., unpublished work) show clearly that the clouds are statically photoionized, presumably by young stars in the Galaxy¹¹. Clouds at even greater distances than the Magellanic Stream — that is, beyond 50 kiloparsecs — should have even weaker ionized hydrogen emission. Much beyond 300 kiloparsecs, it would be very difficult to detect any ionized hydrogen signal at all.

The discovery of dense HVCs with no detectable signal for ionized hydrogen would constitute the first tentative step in demonstrating that there may indeed be a population of primordial gas clouds (with associated dark matter) dispersed throughout the Universe, thereby confirming Blitz and colleagues' hypothesis. These are exciting times for near-field studies of galaxy formation. Several groups around the world are well placed to identify a statistically useful sample of such clouds for closer scrutiny with the new generation of large ground-based and space-based telescopes. Watch this space. □

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Biophysics

Relating dynamics to function

Ann Stock

Movement at the molecular level is essential for macromolecular function. Nonetheless, our images of proteins are dominated by static, three-dimensional structures that give only snapshots of the allowable conformations. One method for studying the structural dynamics of macromolecules in solution is NMR spectroscopy, which is providing increasingly detailed descriptions of the motional parameters in proteins¹. But it is not straightforward to correlate molecular motions with protein activities, and a central question remains — how do dynamics relate to function?

On page 289 of this issue, Feher and Cavanagh² give an insight into this problem with their NMR dynamics study, which characterizes movements in Spo0F, a response-regulator protein involved in a phospho-relay signal-transduction pathway in *Bacillus subtilis*. Feher and Cavanagh find that amino-acid residues moving on microsecond to millisecond timescales in Spo0F correspond to residues that have previously been identified as important in mediating interactions with three other signalling partners^{3,4}. This study adds to the growing list of cases where conformational dynamics are correlated with protein–protein interaction surfaces.

The subject of the study, Spo0F, belongs to a large family of response-regulator proteins that function within two-component signal-transduction pathways⁵. These two-component systems involve a sensor kinase that adds a phosphoryl group to itself (autophosphorylates) at a histidine residue. This creates a high-energy phosphoryl group that is then transferred to a conserved regulatory domain of a response-regulator protein. Two-component systems are modular with respect to both the arrangement of domains within proteins, and to proteins within pathways. But whereas many such systems involve just a sensor kinase and a response regulator, others, such as the *B. subtilis* sporulation pathway in which Spo0F participates⁶, use many phospho-transfer components in a more complex phospho-relay scheme.

The conserved response-regulator domain acts as a phosphorylation-activated switch, in which the phosphorylated form typically corresponds to the active, or 'on', state of the protein. Diverse experimental

data obtained with different response regulators has led to the generally accepted hypothesis that the regulatory domain can exist in two main conformations, with phosphorylation shifting the equilibrium between them. Regulatory domains then modulate the activity of other, 'effector' domains, owing to different protein–protein interactions favoured by the two switch conformations. Unfortunately, the short lifetime of phosphorylated response regulators (typically ranging from seconds to hours) has so far inhibited their direct structural analysis.

Spo0F is a small, 124-amino-acid protein consisting of five α -helices and five β -strands joined by small loop regions. It interacts with three different proteins in the sporulation pathway — its upstream and downstream phospho-relay partners (histidine kinase, KinA, and phosphotransfer protein, Spo0B, respectively), as well as with a phosphatase, RapB. Residues involved in these interactions have been identified by alanine-scanning mutagenesis, and they form a semi-contiguous surface that extends over one face of Spo0F^{3,4}. When Feher and Cavanagh compared this functionally defined surface to their dynamics data, they found a strong correlation.

The authors determined NMR relaxation parameters for most of the backbone amide nitrogens of Spo0F, then they fitted these to dynamic models⁷. They obtained estimates for the magnitude and timescale of backbone motions. The parameters indicate that the α -helices and β -strands in Spo0F (shown, in Fig. 1a and b, as helical ribbons and arrows, respectively) behave rigidly in the picosecond to nanosecond timescale. This contrasts with regions at the amino and carboxy termini, and a loop extending from the phosphorylation site, which undergo fast internal fluctuations. The authors found that regions which experience perturbations in the microsecond to millisecond range form a distinct patch that almost perfectly overlaps the previously defined protein–protein interaction surface (Fig. 1).

How do these micro- to millisecond fluctuations contribute to Spo0F function? This question provides Feher and Cavanagh with a fertile topic for speculation. They address the possibility that the flexibility of regions involved in protein–protein interactions

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, particular-

ly from lakes full of closely related fish species², 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 intermedi-

ates, 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 recombination³, 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 mates⁴. But in general they are not.

Two new theoretical treatments by Kondrashov and Kondrashov⁵ (KK, page 351 of this issue) and Dieckmann and Doebeli⁶ (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

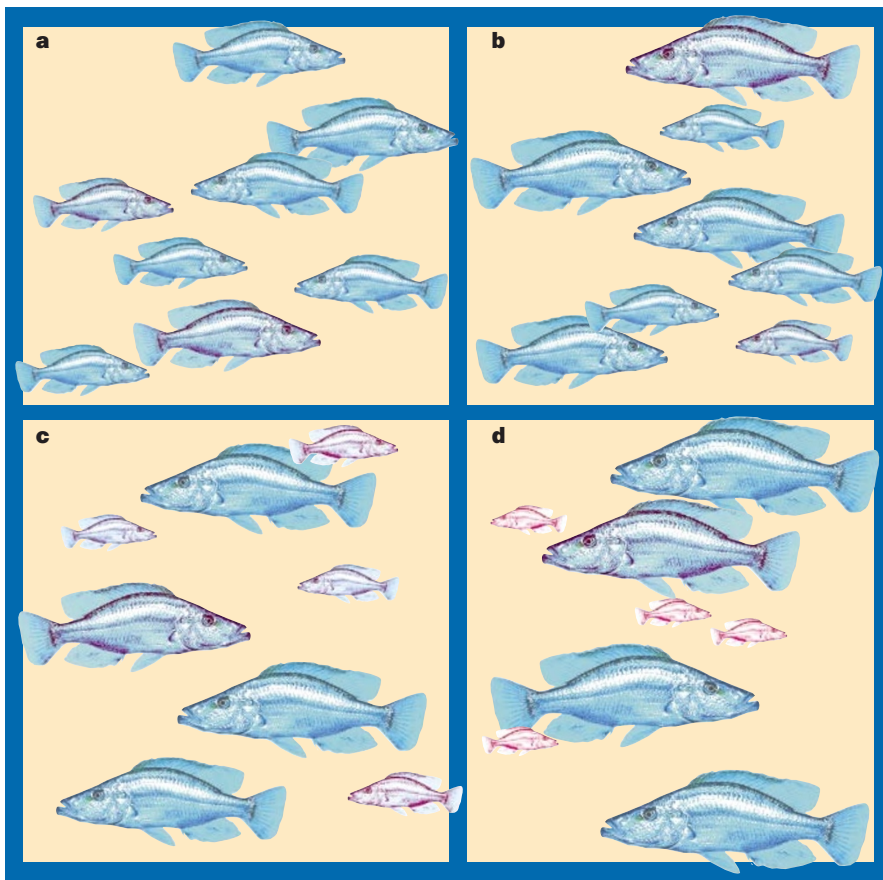


Figure 1 Sympatric speciation according to the KK model⁵. The population is initially uniform for both ecological traits (size) and mating traits (colour), but contains genetic variation for both traits. a, The population rapidly evolves to intermediate size. b, Disruptive selection creates divergence 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 model⁶, 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 lakes⁸; 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 parents⁹. 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 straitjacket¹⁰. □

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Materials science

Superhard ceramics

R. J. Brook

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 issue¹ 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 nitride² (Si₃N₄) 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 Si₃N₄, 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, Si₃N₄ 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 Si₃N₄ is no exception: the precursor material is shaped into a powder mass, which is then