(Jeremy Searle, University of York, UK, and Jean David, CNRS, Gif-sur-Yvette, France), grasshoppers and their kin (Godfrey Hewitt, and Kerry Shaw, Harvard), toads (Jacek Szymura, Jagiellonian University, Krakow, Poland, and Nick Barton, Edinburgh University, UK) and parasitic ticks (Mike Bull, Flinders University, Adelaide, Australia). Although few researchers have the stamina to maintain such long-term programmes, the payoffs from such investments were there for all to see.

For understanding of a field to advance, empirical and theoretical approaches must advance hand-in-hand. Hewitt can take personal credit for attracting some of the most productive minds currently active in this field into the fold (Nick Barton). Such are the intricacies of hybrid zones that their more counterintuitive emergent properties can only be revealed through explicit mathematical models. For the less mathematical among us this means watching hybrid zones evolve before us in a blizzard of lambdas.

The impressive thing about this meeting was how great a diversity of approach and study taxa was represented (too many, sadly, to cover in full here). Phylogeography was christened as a field by Avise and he could rightly lay claim to be its father figure. Over a similar evolutionary timescale, Hewitt has been an influential godfather, with much still to offer.

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JOURNAL CLUB

Conservation and mutability in molecular evolution

DNA polymerase, the enzyme responsible for DNA replication, has highly conserved functional domains that have been maintained over billions of years of evolution. The 13 amino acid sequence of 'motif A' is identical across highly divergent bacterial lineages and retains the same structural identity from prokaryotes to mammals. The exceedingly slow evolution of motif A suggests that any change results in intolerable disruption to polymerase function. However, Premal Patel and Lawrence Loeb[1] have challenged this simple concept of sequence conservation by demonstrating that virtually any amino acid in the motif can be mutated without apparent loss of polymerase function.

To investigate the plasticity of the polymerase active site, the authors randomly mutated the DNA sequence that codes for motif A in the bacterium *Thermus aquaticus* (from which the Taq polymerase used in DNA sequencing is derived). By selecting for mutants that were capable of DNA polymerase activity, they generated a surprisingly large library of around 8000 physiologically active mutant polymerases. Characterization of a random subset of 350 of these revealed that the majority had polymerase activity that was comparable with the wild type, and bacteria that were dependent on these mutant polymerases were able to survive and replicate for >50 generations. All but one of the amino acid residues in motif A could be changed without substantial loss of polymerase activity, including one active mutant polymerase with amino acid changes in 6 of the 13 residues. Perplexingly, a serine residue present in motif A in nearly all eukaryotes and prokaryotes proved highly mutable, able to accept a diverse range of amino acid substitutions.

These results present a conundrum. The dramatic conservation of the amino acid sequence suggests that motif A is functionally immutable. However, these experiments suggest that motif A can function with a wide range of amino acid substitutions. How can these two contradictory observations be reconciled? The authors reject the possibility that Taq polymerase might be unusually plastic, citing other polymerases that seem equally mutable. Clearly, the comparatively easy life of bacteria growing in a laboratory culture might not reveal tiny differences in polymerase activity that could provide a selective edge in the real world. However, the authors favour the hypothesis that the observed mutability allows survival and adaptation during harsh times when mutators might be favoured, but that motif A then returns to the conserved sequence by genetic transfer. Whatever the explanation, Patel and Loeb have demonstrated that we should think twice before assuming a simple connection between sequence conservation, mutability and functional importance. As is so often the case, molecular evolution turns out to be far more complex than we first thought.

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Reference

1 Patel, P.H. and Loeb, L.A. (2000) DNA polymerase active site is highly mutable: evolutionary consequences. *Proc. Natl. Acad. Sci. U. S. A.* 97, 5095–5100

Displaced characters get some space

Despite its central place in ecological and evolutionary theories, the phenomenon of competition has seen many of its facets wax and wane over the past few decades. Two papers[1,2] just published in *The American Naturalist* might well rekindle research on the phenomenon of 'character displacement' – the observation that species have evolved to be less like one another when coexisting (sympatry) than when isolated (allopatry).

Character displacement is one of the arrows in the quiver of the ecologist and the evolutionary biologist, providing evidence that interspecific competition exists or at least has existed in the distant past. The generally accepted requirement for character displacement to occur is that no single competitor will exploit the full pool of resources exploitable by the full community of competitors. Essentially, species in sympatry pay a cost in evolving components of their habitual ecological niches so as to reduce the otherwise greater costs of competition. Curiously, until now, theory has generally overlooked the empirical fact that character displacement is a spatial phenomenon. As such, most of our current understanding of character displacement is based on situations where all competitors are confronted with the same resource pool – although plausible, this is probably the exception rather than the rule. Therefore, the theory needs explicit spatial distributions of competitors and resources. The two *American Naturalist* articles address the same basic problem from rather different angles.

Troy Day[1] reduced space to two interconnected patches, each with a distribution of resource types. Employing a game-theory approach of evolutionary optimization, he found that heterogeneity tends to promote differentiation when migration rates are low and impede it when they are high. Ted Case and Mark Taper[2] use a continuous environmental gradient with competitor evolution dictated by quantitative

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