

NEWS AND VIEWS

MEETING REVIEW

The genetic basis of evolution, adaptation and speciation

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A primary question in biology concerns the genetic basis of the evolution of novel traits, often in response to environmental changes, and how this can subsequently cause species isolation. This topic was the focus of the symposium on the Genetics of Speciation and Evolution at the annual meeting of the Canadian Society for Ecology and Evolution, held in Banff in May 2011. The presentations revealed some of the rapid advances being made in understanding the genetic basis of adaptation and speciation, as well as the elegant interplay between an organism's genetic complement and the environment that organism experiences.

Keywords: adaptation, ecological genetics, molecular evolution, speciation

Received 10 August 2011; revision received 28 September 2011; accepted 29 September 2011

The field of evolutionary genetics has seen dramatic advances in recent years, as genomic tools have become more accessible and refined. The increasing ease of developing genetic tools in a new system has opened the door for genetic studies in a variety of organisms, allowing researchers to choose their model system based on its relevance to the question at hand rather than on the existing availability of genome sequence. This trend was readily apparent from the series of presentations in the Genetics of Speciation and Evolution symposium. The unifying theme was not a particular model system, but rather how an organism's genomic complement influences its ability to maintain species boundaries and adapt to new environments.

The genetical biogeography of speciation

Among biologists, there remains a dispute about the likelihood of speciation occurring in the face of complete gene

flow: sympatric speciation. One confounding factor is in how researchers define sympatric speciation, specifically, whether it should be approached from a genetic or a biogeographic perspective. Jerry Coyne (University of Chicago) presented a critical review of the evidence for sympatric speciation. Although there are some examples that appropriately fit the biogeographic definition of 'speciation occurring in a small area' (e.g. Sorenson *et al.* 2003; Mavárez *et al.* 2006), they display 'genetic trickery,' with factors that limit the possibility of gene flow from the outset. Thus, these examples fail the genetic definition of sympatric speciation, which involves not just speciation in a small area, but speciation in the face of pervasive gene flow. Using this genetic definition, sympatric speciation still remains controversial and poorly supported. This contrast encourages evolutionary biologists to clarify the focus of their work, either on the biogeographic aspects of speciation or on the relationship between gene flow and selection during speciation.

Testing the genomic island model of species isolation

The genetic basis of species boundaries can be explained by two different models: speciation by individual genes or speciation because of genomic islands. In the latter, divergent hitchhiking causes a decrease in interpopulation recombination because of selection against immigrant alleles, and thus plays an important role in the formation of good species. Louis Bernatchez (Université Laval) and his colleagues evaluated the likelihood of genomic islands causing speciation in young populations of whitefish (*Coregonus clupeaformis*). They performed genetic mapping in multiple sympatric populations with different degrees of divergence and identified candidate regions for divergence between the two species (Renaut *et al.* 2011). They found that divergent selection is more likely to be acting on regions of the genome that influence adaptive phenotype than regions that do not. A comparison of the genomic regions' sizes between populations found large islands of divergence, providing support for the genomic island model of speciation. These islands generally increased in number and size as divergence intensity increased, as would be expected if divergence is driven by the same forces as ecological adaptation. Continued comparisons of genomic and ecological findings in whitefish populations will lead to a greater understanding of how speciation occurred and how these species are maintained, despite ongoing gene flow.

Another aspect of the genomic islands concept that may explain speciation lies in an increasing number of genomic islands rather than in their increasing size. By comparing different populations of sunflowers (*Helianthus*) at varying

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degrees of reproductive isolation, Loren Rieseberg (University of British Columbia) and his colleagues were able to analyse the size of genomic islands and where they occur during differentiation (Yatabe *et al.* 2007; Scascitelli *et al.* 2010). They compared species pairs with different divergence times and levels of gene flow to evaluate how gene flow and genetic hitchhiking may lead to differences in island size and number. Interestingly, all species pairs had a similar number of small islands of differentiation regardless of whether they were sympatric or allopatric, with a greater number of small islands in more divergent species pairs. The genomic location of islands was also consistent across all four comparisons with gene-dense areas being far more likely to exhibit differentiation, suggesting that the same genomic regions may be repeatedly involved in sunflower speciation. These results provide evidence that the expanding island number model may play a pivotal role in speciation.

Genetic architecture of a hybrid zone

Although biological species are reproductively isolated by definition, naturally occurring interspecific hybrids are commonly found and can allow genetic exchange across species boundaries (Martinsen *et al.* 2001). In plants, this exchange of alleles may occur at climatic transitional zones in which two closely related species overlap and form hybrids. Jill Hamilton (University of British Columbia) presented her work on the genetic mechanisms underlying local adaptation in a naturally occurring Sitka (*Picea sitchensis*) and white spruce (*P. glauca*) zone of introgression. A low amount of hybrid heterozygosity indicated a hybrid zone primarily comprised of advanced-generation recombinants, where weak barriers to reproduction exist between species, although there was an asymmetrical excess of Sitka spruce ancestry. Hybrids were more tolerant than pure species to moderately cold temperatures (a key fitness trait in boreal and temperate trees), but this advantage was lost at severely cold temperatures. While most phenotypic variation did not correlate with climatic gradients, there was clinal variation in the hybrid index, indicating that the local environment strongly impacted the genetic structure of the hybrid zone. Thus, environmental selection may shape the genetic make-up of hybrid transitional zones.

Quest for the origin of species

Reproductive isolation plays an important role in the origin of species; however, the genetic basis of reproductive isolation is largely unknown. An ongoing study in Dolph Schluter's laboratory (University of British Columbia) and Catherine Peichel's laboratory (Fred Hutchinson Cancer Research Center, Seattle) examines the genetic basis of isolation between the recently evolved and sympatric benthic (feed in shallow water) and limnetic (feed off-shore near the lake surface) stickleback species pairs. These species mate assortatively by body size, which is thought to be an adaptation to their preferred benthic or limnetic habitat

(Nagel & Schluter 1998; Rundle *et al.* 2000). Benthic, limnetic and F2 hybrids of stickleback species arising from different lakes were housed in large experimental ponds, assayed for habitat preference and body size, and then genotyped at molecular markers. Preliminary results show that genes influencing habitat selection localize to the same region of the genome that also influences body shape differences between the two species. Thus, the genes for habitat preference and ecological adaptation are in close physical linkage on a chromosome. Given the repeated and rapid evolution of stickleback species pairs, future studies will aim to address whether the same genes are selected for repeatedly in independently evolved species pairs.

A genetic locus for behavioural isolation

Although behavioural isolation is arguably thought to be the first step in speciation (Coyne & Orr 1998), no genes have been directly linked to behavioural isolation. Amanda Moehring (University of Western Ontario) presented the work carried out by graduate student Meghan Laturney on identifying the first candidate gene for behavioural isolation between two species of *Drosophila*. Using female flies that were missing small portions (genome deficiencies) of one chromosome arm, they mapped regions of the genome contributing to a female's unwillingness to mate with males of another species. Small, overlapping deficiencies within each significant region were used to refine the region, and then individual candidate genes within this refinement were tested, one of which was significant. The gene for female preference, which they named *It's not you it's me* (*Ntu*), produces a microtubule-binding protein. The researchers suggest that the different alleles in the two species affect a female's behaviour through the gene's effects on axon patterning in the brain. Further tests will confirm whether this is true and will also determine whether similar genes act to influence behavioural isolation in related species pairs.

Evaluating the 'lock-and-key' model

Sometimes, the environment that influences an organism's evolution is the members of the opposite sex. One aspect of this is genital shape evolution. Physical incompatibility of genitalia is one mechanism postulated to prevent interspecies mating: the male 'key' might not fit the female 'lock'; for example, the widely studied species-specific shape of the male genital arch in *Drosophila mauritiana*, which is external to the penis, is thought to reduce copulation duration when these males are paired with females of *D. simulans* (Robertson 1988). Historically, the difficulty of manipulating genital structures in live organisms has precluded most empirical tests of the 'lock-and-key' hypothesis. Hélène LeVasseur-Viens (University of Western Ontario) used a micro-dissection laser to alter the male genital arch of *D. simulans* males to varying degrees and then measured whether these alterations reduced their copulation duration with *D. simulans* females. These males

displayed normal conspecific courtship behaviours, but their genital arch shape was altered to no longer be conspecific. Surprisingly, these altered males did not suffer reduced copulation duration as expected. LeVasseur-Viens then examined the timing of unaltered male's insertion of its penis into the female after they were coupled and found that the two species have different insertion times, and hence this timing (rather than morphology) may be what is used for female discrimination.

The evolution of sex during adaptation

Many hypotheses have been proposed to explain how sexual reproduction, despite its obvious costs, originated and is maintained. The prevailing theory states that sex is favoured during adaptation and when there is a long-term advantage (Weismann 1889); however, there is little direct experimental support for this theory. Lutz Becks and Aneil Agrawal (University of Toronto) used facultative sexual rotifers (*Brachionus calyciflorus*) to test the theory that sex is more likely to evolve in novel environments, wherein adaptation pressures are present. Although the rate of sex initially increased when adaptation pressures increased, it later tapered off, suggesting that the benefits of sex are transient. This still leaves the question: Why have sex? Sex increases the variance of genotypes, which can have long-term advantages. Therefore, despite its obvious short-term disadvantages, it is possible that sex evolved because of its long-term advantages, such as the associated increase in genotypic variance. The results described suggest that recurrent changes in the environment, leading to a continuous state of adaptation, must occur for sexual reproduction to be rampant.

The genetic basis of local adaptation

Hopi Hoekstra (Harvard University) presented her laboratory's work on the genetic basis of coat colour variation in two populations of old field mice (*Peromyscus polionotus*): a dark brown population living on dark loamy inland soil and a light brown population living on pale coastal sand dunes. First, using different-coloured plasticine mice placed in the two habitats, they confirmed that cryptic coloration decreased predation attempts (Vignieri *et al.* 2010). Second, genetic mapping showed that the coat colour variation is controlled by at least three genetic regions. All three genes act together in the same pathway, but their effect on coat colour is via different genetic changes: one has an amino acid polymorphism that reduces protein function, and the other two have a sequence polymorphism affecting gene regulation (Steiner *et al.* 2007). In the latter case, they showed how small changes in gene expression during embryogenesis can cause large changes in adult colour pattern (Manceau *et al.* 2011). Phenotypic differentiation in coat colour is, therefore, caused by multiple genetic changes within the same pathway, whose epistatic interactions have likely led to ecological adaptation.

Exploiting molecular hyperdiversity

Previously, all cases of measured variation at the nucleotide level found extremely low intraspecific molecular diversity, the only exceptions being in viruses and bacteria. Asher Cutter (University of Toronto) presented his laboratory's work on the discovery of hyperdiversity in one species of eukaryotic nematode in the genus *Caenorhabditis* and discussed its implications for genome evolution and potential adaptation to divergent environments. In this species, he found that differences in recombination rates were strongly coupled with levels of nucleotide polymorphism, indicating that regions of high recombination may subsequently be more likely to be influenced by natural selection (Cutter & Choi 2010). In ongoing studies, he is seeking to clarify the poorly understood intraspecific molecular evolution of small RNA genes, the micro-RNAs. Many of these genes are extremely well conserved across animals, which makes exploring their micro-evolution challenging. The hyperdiversity of *Caenorhabditis* species provides Cutter's group a handle to explore differential selection within and among micro-RNAs in contemporary populations. To further elucidate genome organization and evolution, the Cutter laboratory is currently sequencing the genomes of multiple individuals to examine high-resolution genome-wide polymorphism and divergence.

Speciation and adaptation: the final frontier

In conclusion, our understanding of the genetic basis of adaptation and speciation has progressed dramatically in recent years, primarily because of the increasing availability of genetic tools in a range of organisms. We now know some of the physical and genetic changes that can lead to ecological adaptation and speciation. Like most topics in evolutionary biology, the end goal is to understand how evolution progresses in a broader sense, and thus the question remains as to whether these changes are typical or are only present in the one (or few) species examined to date. With the recent dramatic rise in available model genetic systems, we may be able to address not just the genetic basis of these traits but also whether particular genetic pathways or types of genetic changes are universally involved in speciation and adaptation.

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- V.M. investigates the genetic linkage between male traits and female preferences that isolate species. H.L.-V. studies genital morphology and the lock-and-key hypothesis. R.K. examines trends in sperm morphology and how it relates to interspecies hybrid sterility. M.L. investigates the genetic basis of behavioural isolation between species. A.M. is interested in the genetic basis of species isolation.
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- doi: 10.1111/j.1365-294X.2011.05348.x