

NEWS AND VIEWS

PERSPECTIVE

Contemporary hybrid speciation in sculpins (*Cottus* spp.)

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Natural hybridization between closely related taxa is frequent in many organismal groups, yet it has long been perceived as a force preventing diversification and speciation, especially so in animals. In recent years, growing evidence in favour of hybridization facilitating adaptive divergence has accumulated (Mallet 2007; Mavárez & Linares 2008; Nolte & Tautz 2010). Homoploid hybrid speciation (the formation of hybrid lineages without changes in chromosome number) occurs when distinct species come into contact, hybridize, and at least in part of their range, produce hybrid swarms. If the hybrid genotypes can then colonize areas of the adaptive landscape inaccessible to ancestral species, they may eventually form new distinct lineages, reproductively isolated from their ancestors. Invasive sculpins (*Cottus* sp.) are one of a few good examples of homoploid hybrid speciation in animals. In this issue, Stenshorn *et al.* (2011) identified three distinct hybrid lineages, which have emerged out of a secondary contact situation of *Cottus rhenanus* and *Cottus perifretum*. Hybrids have recently invaded large river habitats unsuitable to ancestral species. Through the use of genetic mapping, the authors established that contrary to expectations, chromosomal rearrangements were not apparent in the hybrid lineages. In addition, different population genetic models were tested and the results suggest that contemporary gene flow from ancestral species represents an important component of the system. As such, recent and ongoing hybridization appears to be promoting the appearance of phenotypes adapted to novel environments. The examination of partially isolated lineages such as invasive hybrid sculpins should permit to identify early adaptive genetic changes before they become confounded by differences arising once speciation is complete.

Keywords: adaptive divergence, *Cottus*, hybridization, reproductive isolation, sculpins, speciation

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The poster child of homoploid hybrid speciation, which has set standards in the field, is the sunflower. Three novel spe-

cies, ecologically specialized into extreme habitats, arose via hybridization between *Helianthus annuus* and *Helianthus petiolaris*, and much of what we understand about hybrid speciation comes as a legacy of work on this system (Rieseberg *et al.* 2003). Unfortunately, far less is known in animals, with one of the few recognized examples being the invasive hybrid lineages of *Cottus* in Europe (Nolte *et al.* 2005). The primary habitats of *Cottus* are small well-oxygenated headwater or tributary streams, either in the Rhine water system for *C. rhenanus* or the Scheldt water system for *C. perifretum*. These two water systems were separated until about 200 years ago when artificial canals were dug in the Netherlands. This, in turn has favoured the secondary contact and subsequent hybridization of the species. Hybrid lineages, possessing new ecological adaptations invaded large stagnant water bodies such as the Rhine River in Germany, a habitat inaccessible to either *C. rhenanus* or *C. perifretum* (Fig. 1). Stenshorn *et al.* (2011) constructed distance trees and performed principal component analysis using 81 ancestry informative single nucleotide polymorphisms (SNPs) to reveal that the hybrids' distribution consisted of three distinct lineages. Surprisingly, individuals of the same genetic group occurred at geographically distant locations, while geographically adjacent groups were sometimes genetically different. It seems likely, as in sunflowers, that hybridization has facilitated divergence, which then contributed to the onset of reproductive isolation between groups of individuals adapted to different ecological conditions. However in this case, hybridization is far more recent (less than 200 generations) and consequently, contemporary gene flow is still an inherent characteristic of the system. In fact, Stenshorn *et al.* (2011) modelled three different population genetics scenarios describing how a hybrid gene pool could emerge from the hybridization of the two species. The most parsimonious model suggested that a combination of initial admixture combined with secondary gene flow best explained the contemporary situation of the hybrid lineages. In addition, only two SNP markers deviated from a neutral model of divergence, implying that few genetic changes underlie the ecological differentiation of the hybrid lineages. Using SNP markers, especially if these can be linked to genes of interest in a natural setting as this one, should reveal how each lineage's integrity is maintained in the face of ongoing gene flow.

Certainly, the nature, size and genomic distribution of genes maintaining and promoting reproductive isolation (so-called *speciation* genes) are still a matter of debate in the scientific community. The genic view of speciation posits that genomes are porous and only certain circumscribed regions or genomic island of divergence should cause reproductive isolation (Wu 2001). In addition, these regions may differ between phenotypically or ecologically similar populations either through the recruitment of different



Fig. 1 Bottom right picture depicts the typical ancestral habitat (small cool streams), while upper left illustrates the habitat recently invaded by the hybrids (large warm rivers such as the Rhine). The upper right picture shows a representative sculpin phenotype, while the lower left is a male in black breeding coloration guarding its territory.

mutations in parallel systems or because of selective pressures varying between sites. In fact, recent analyses of two hybrid zones between invasive and resident sculpins have provided little evidence of parallelism at the genetic level supporting the independent evolution of different hybrid lineages (Nolte *et al.* 2009).

Again, based on the work carried out in hybrid sunflowers, chromosomal rearrangements are often thought to be an essential aspect promoting hybrid speciation. Rearrangements should impede gene flow through the suppression of recombination around the chromosomal breakpoints, thus promoting regions of divergence and ultimately facilitating speciation (Rieseberg 2001). While plausible, this idea remains difficult to test and few examples directly support their role in the initial sorting of hybrid lineages. Here, Stemshorn *et al.* (2011) rejected the hypothesis that chromosomal rearrangements facilitated the reduction of gene flow between lineages. Based on an initial draft of a *Cottus* genetic map (Stemshorn *et al.* 2005) whereas certain markers were suspected to be in rearranged regions of the genome, the authors created five distinct pure invasive and five pure *C. rhenanus* families. Then, they genotyped 49 microsatellite markers in order to demonstrate that the maps for the invasive hybrid lineages and the pure *C. rhenanus* were in full concordance. Of course the map contained relatively few markers, but should be enough to rule out large chromosomal rearrangements. Genetic mapping requires long-term planning and careful experimental sampling, a task few have performed in the context of a recent speciation event. Further refined mapping efforts will undoubtedly provide better clues as to the intricate ways the genomic architecture of these lineages are moulded by hybridization. Indisputably the authors have presented here and in previous work on this system, extensive ecological and genomic data, bringing the gap between these two disciplines. This in turn will help to clarify the respective role of hybridization, gene flow and selection in promoting divergence and ultimately, speciation.

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