Hybrid zone dynamics in amphibians

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Summary

Hybrid zones occur where two species meet and produce offspring (hybrids). Typically, hybrids show a considerable reduction in fitness. When two species have diverged in allopatry (different geographic locations), meet again after they expand their distributions, and if the two are not yet completely reproductively isolated, the hybrid zone classifies as a secondary contact. Newly evolved gene variants of one species may be incompatible with the gene variants in the other species, and may underlie (incomplete) reproductive isolation. When such incompatibilities become linked in the genome, e.g. because they are located on the same stretch of DNA, or are distributed throughout all the parental populations, they may cause a genome-wide reduction of gene flow between the two species, compared to the dispersal rate of individuals. This is referred to as the 'barrier effect'. The genes that underlie the barrier effect may also be called 'barrier genes'.

In the classic hybrid zone literature, hybrid zones are thought to stabilise (geographically) soon after they are formed. However, recent studies show that hybrid zones can shift across considerable distances after their formation. During hybrid zone movement, one species replaces the other because of a fitness advantage of one of the species over the other. A genetic footprint of neutral gene variants of the displaced species remaining in populations that have been overtaken by other species would provide evidence of hybrid zone movement.

During meiosis (egg or sperm formation) genes segregate and randomly combine again at fertilization. During this process, the DNA can break and be recombined, resulting in new combinations of genes. Linkage disequilibrium is the association of multiple genes, and decays with segregation and recombination. The closer two gene variants are on a chromosome, the less likely recombination will take place. Genes which are different between two species involved in a hybrid zone, show a peak of linkage disequilibrium in the hybrid zone centre. The position of this peak indicates where, geographically, recombination of the parental species' genes has taken place the least during hybridisation. If a hybrid zone moves, this peak is expected to be positioned on the side of the hybrid zone in the direction of movement. In this thesis, two potentially dynamic hybrid zones are studied to further characterise the genetic footprint and expected peak of linkage disequilibrium caused by hybrid zone movement.

Two species of banded newts (*Ommatotriton nesterovi* and *O. ophryticus*) are thought to meet in a hybrid zone in the north of Turkey. The two other pairs of salamander species in this region (*Triturus anatolicus* and *T. ivanbureschi*, and *Lissotriton vulgaris* and *L. kosswigi*) show a genetic footprint due to hybrid zone movement over hundreds of kilometres. In this thesis I confirm the species status of the two banded newt species based on mitochondrial DNA and two nuclear DNA sequences. The location of the hybrid zone is narrowed down to a 60 km wide region where no samples were available. No genetic footprint is found within the natural distribution outside of this 60 km wide region. Thus, if a hybrid zone is present between *O. nesterovi* and *O. ophryticus*, it is narrower than 60 km and it may be geographically stable. An introduced population of hybrid banded newts in Spain provides evidence that the two species can produce fertile offspring. This increases the likelihood that a hybrid zone indeed exists between the two species.

Common and spined toads (*Bufo bufo* and *B. spinosus*) meet in an 800 km long hybrid zone that runs diagonally across France. A genetic footprint north of the hybrid zone was previously recorded and linked to southward hybrid zone movement, with *B. bufo* overtaking *B. spinosus.* To test hypotheses of hybrid zone movement, a transect in northwest France was studied with 31 nuclear markers. A genomic footprint towards the north indicated southward movement, whilst a peak of linkage disequilibrium in the north is in line with northward movement. The contrasting results suggest that stronger reproductive isolation on the *B. spinosus* side of the hybrid zone than on the *B. bufo* side, may be more likely than hybrid zone movement.

Replication of transects along a hybrid zone helps to identify factors driving hybrid zone movement. Two distant transects, one in the northwest and one in the southeast of France, were studied using 1200 nuclear markers. Asymmetries which were previously found in the literature and in this thesis, were confirmed for the hybrid zone in northwest France, but not in the southeast, where the gene flow appears to be symmetric, indicating the hybrid zone is stable here. Barrier markers, genetic regions which may be associated with barrier genes, were identified by their relatively restricted gene flow. The number of shared markers which behave as a barrier marker in both transects is higher than expected when the barrier effect was established in each transect separately. This overlap suggests that the two species have evolved a universal genetic barrier to gene flow. The differences in patterns of gene flow between the transects may be caused by genetic divergence within *B. bufo,* documented in previous phylogeographical work.

We clearly can no longer think of hybrid zones as static upon formation; hybrid zones evolve! The position of a peak of linkage disequilibrium generated testable hypotheses, but many questions remain about what is expected for the shape and position of this peak under different scenarios of hybrid zone movement. With the increasing availability of genome resources, detection of more detailed patterns of differential introgression along the genome in hybrid zone studies will reveal the genetic architecture of speciation and the evolution of hybrid zones.