

Genome Reticulation and Cytonuclear Coevolution in Hares (*Lepus* spp.)

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The mitochondrial genome has been the most studied in evolutionary biology, but the relationship between variation and functional evolution and the coevolution with the nuclear genome remain little documented and tested. Hares, genus *Lepus*, are emerging as particularly suited models to tackle this question. The Iberian hare, *Lepus granatensis*, harbors high frequencies of mitochondrial DNA (mtDNA) from *Lepus timidus* in the north of its distribution in the Iberian Peninsula but not in the south. The latter species is widely distributed in the Northern Palaearctic and went extinct from Iberia at the end of the last glacial period, as attested by the fossil record. Thus, the mtDNA introgression found in Iberia results from ancient hybridization between *L. granatensis* and *L. timidus* when the species coexisted in the region. Gene flow also affected other genomic compartments, such as the autosomes and the X chromosome. Nevertheless, mtDNA introgression is the most spectacular between these taxa, and is the only that is geographically structured, suggesting that it may be related with environmental variables. Also, population genetics studies suggest that some of the patterns of introgression inferred in *L. granatensis* are difficult to reconcile with purely neutral processes. Since mtDNA and nuclear encoded peptides closely interact in metabolic functions and *L. timidus* is well adapted to cold, mtDNA introgression may have had a functional impact. We asked whether the strong north-south differentiation for mtDNA in *L. granatensis* is paralleled by some nuclear genes, as a result of either cointrogression with mtDNA or evolution after introgression. If genes with such patterns were preferentially involved in interactions with mtDNA genes, we would have a strong case for coevolution between the two genomes, for the functional role of mtDNA variation, and perhaps for the adaptive nature of interspecific mtDNA introgression. We analyzed transcriptome sequence data from five *L. granatensis* sampled in northern populations where mtDNA introgression is pervasive, and five in southern populations where introgression is absent, and also from a pool of three *L. timidus*. Sequence variation of over 3000 nuclear genes generally revealed low differentiation between northern and southern samples, with average F_{ST} close to zero. However, a small subset of genes presented high levels of geographic structure, and some had variation consistent with introgression from *L. timidus*. These results suggest that introgression of nuclear genes co-occurred with mtDNA but affected a small number of genes. Interestingly, a gene ontology analysis revealed a significant excess of functions related with mitochondria and metabolism in the 1% of nuclear genes with the highest F_{ST} , which suggests adaptive coevolution between the mitochondrial and nuclear genomes, accompanying introgression of mtDNA.

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