

SPECIES ON THE EDGE OF MERGING

Dmytro Kryvokhyzha

A species is usually considered to be a group of organisms that can breed among themselves but cannot reproduce with individuals from other species. Thus, the main criterion of a species has been reproductive isolation. This concept has been subtly modified during recent decades after hybridization between species was proved to play an important role in the evolution of some species. Hybridization can result in the transfer of advantageous genes from one species to another. For example, antibiotic resistance genes have frequently been transferred among bacterial species. Sometimes, hybridization can lead to the formation of a completely new species. Instead of being merely intermediate, hybrid progeny can acquire new adaptations that allow them to proliferate and survive in ecological settings where the parental species are poorly adapted. Inter-species hybridization is also widely employed to combine useful variation in crop breeding. Moreover, there is growing evidence that hybridization impacted even the evolution of the human genome. These and many other examples indicate that hybridization is a more important evolutionary phenomenon than previously believed. In this study, we describe a case where hybridization has obliterated many of the differences between a pair of species, even though the species boundary is still maintained by a small fraction of the genome.

We investigated the genomes of a pair of sister species of tropical butterflies *Heliconius elevatus* and *Heliconius pardalinus*. The species fly together across much of the Amazon river basin, although in some areas near the edge of the Amazon, only one of the two species occurs. To all appearances, these very different-looking butterflies are normal species, although occasionally (maybe one in a thousand or one in ten thousand specimens collected) hybrids between the two occur in the wild. We sequenced the DNA of the complete genetic material (genome) of each of these species from areas where they co-occur, and from areas where each occurs alone. We found, to our surprise, that where *H. pardalinus* and *H. elevatus* overlap, the two species are more closely related to each other than they are to members of their own species from other regions. This seemed odd, given that the two species were not previously considered to be particularly closely related. They are very distinct in their coloration, body size and flight behavior.

Even when we scanned across the genome in small chunks, there were almost no differences between these two species in the Amazon. However, about 1-2% of the genome did show major differences between the species, representing narrow regions of divergence on only 13 out of the 21 chromosomes. When we examined the genetic relationships among populations using only these regions of divergence, all populations of *H. elevatus* and *H. pardalinus* fell into two clearly separate groups belonging to the correct species. This conforms to the traditional species designations, and shows that the two species had indeed split some time ago. The close relationship of the other 98% of the genome where the two species overlap in the Amazon is therefore most likely explained by more recent genomic mixing caused by occasional hybridization. The genes situated in the regions of divergence turn out to be involved in formation of wing color patterns and odour detection. It is likely that these characteristics play a key role in mating behavior, and maintenance of species separateness.

We conclude that the ongoing exchange of genetic material between these two species has led to their almost complete homogenization in the Amazon. However, the boundary between these species is still well demarcated by differences at only a few genes that control the appearance and behavior of these butterflies.

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Biology Education Centre, Uppsala University, and Department of Organismic and Evolutionary

Biology, Harvard University, USA

Supervisors: James Mallet and Hans Ellegren